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SOCIAL STRUCTURE OF A COLONY OF *Macaca mulatta*

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Introduction

Certain aspects of the social behaviour of *Macaca mulatta* have been selected for study because of important conclusions about subhuman primate societies which have been reached in the earlier work. The work of Zuckerman (1932) and Carpenter (1942) has placed in the forefront of our ideas the fact that the existence of a dominance hierarchy of adult males is related to the prominence of mating behaviour. The prominence of mating behaviour is itself a consequence of the fact that a large proportion of the reproductive cycle in the female is occupied by (oestrus) receptivity (Chance & Mead, 1952). The dominance relations in Macaques as well as Baboons (Zuckerman, 1932) are, therefore, conspicuous by being constantly present and as a result influence every aspect of behaviour. Dominance gives priority of access. The probability, therefore, of access to an incentive appropriate to a monkey's activated drive may be expected to depend upon the degree of dominance exerted by that monkey. In this situation every motivated activity will engender a conflict, the resolution of which is the result of stereotyped forms of behaviour, or behaviour which has been learnt in the context of the particular society in which the monkey lives. The present study was undertaken to find out methods by which these two aspects of the individual response to conflict could be identified for separate study and to characterise the nature and degree of these social conflicts in macaque society.

As a first step, it was essential to work out satisfactory methods of recording (*a*) the individual and (*b*) the inter-individual behaviour of animals in colonies, and then, to identify and describe the characteristic social behaviour patterns of the macaque monkey. Finally, a detailed working hypothesis to explain the spatial relationships between animals of the breeding hierarchy is obligatory in a study of each primate species, since only within a framework of social cohesion can the individual's behaviour be interpreted.

Methods of Study

1. General observation and description of events as the observer noticed them (soon discarded in this study).

2. Attention was centred on the dominant set or particular groups of animals. Ritual or other *episodes* were observed as they occurred and were described from memory immediately afterwards (checking back the description immediately against a second observer wherever possible).

3. An animal was selected and the behaviour described. The behaviour was summarised at least every two minutes. *Episodes** from the description were selected at leisure afterwards, (supplementing these by the record made at the time by the second observer). This method was more accurate because attention was not divided, a reference point for all description was fixed and familiarity with the animal, which was obtained by observing the animal for 5 minutes before recording started, greatly facilitated observation. Moreover, this is the only way by which intention movements heralding particular forms of behaviour can be observed.

The colony was established in April, 1952, by the liberation of 253 rhesus monkeys on to Monkey Hill at the "Zoological Gardens," Regents Park, London. This is a concrete, oval pit, approximately 30 × 50 yards, sunk approximately 12 feet below the edge of the parapet. The centre is raised so that a moat surrounds a plateau at ground level, from which rise two mounds approximately 15 feet high and 10 feet in diameter. The colony was observed weekly from then until the end of June, when Mr. G. Horn observed the colony daily until July 26th. From then onwards there was a gap during August, when only a few observations were made, and subsequently two observers were present every day from September 1st until September 15th. From then until the end of October the colony was observed on three separate occasions.

The identity of the adult males is here denoted by the letters D1, D2 and D3, etc., indicating their position in the male hierarchy. The adult females were not similarly identified, but are mentioned as and when they were observed in association with particular males.

**Episodes* arise when an animal enters into relations with one or more other animals in such a way that its behaviour is related to the same animals in an uninterrupted sequence of acts.

TYPES OF BEHAVIOUR

I. Sounds

(a) Eech

This sound was a shrill repetitive cry given with the mouth drawn back to its limit. It frequently lasted 10 to 15 seconds but might last as long as half a minute, and occurred most frequently after an animal had been attacked, or was being attacked, or had been threatened. It was emitted in bursts, often long after the attack or threat had passed (and seemed in these circumstances often to be a response to pain). The sound was rarely, if ever, given by an animal in flight, but was frequently emitted during equilibration (see below) to severe threat. Only on one occasion did it evoke a response in another animal, and this occurred after the sound had been given by a young monkey and had changed to Ee-O, when a female clasped the young animal to its front. (The highest incidence was amongst small and middle size animals; it was emitted only rarely by adult animals).

(b) Ee-O.

Infrequent.

(c) Coo-Coo.

Given by many animals simultaneously (i) in anticipation of food, or when dustbins were rattled by Chimps or workmen; (ii) less often and in less vigorous manner on cold, cloudy days when a break in the cloud let through a shaft of warm sunlight. Almost exclusively restricted to small and middle size individuals, but on one or two occasions larger animals cooed.

(d) Hough-Hough

This was a component of the threat gestures, and was added to the sequence of gestures listed below up to, but not after, No. 3 (see below). It *appeared* to evoke and direct similar threat from nearby animals on to the threatening individual. The effect was very striking, and indeed produced a stirring chorus when 20 or 30 individuals all threatened and gave this call for a brief interval in unison, directed towards an aggression by a dominant animal. This concerted threat happened occasionally when a large number of animals were close together and always terminated the attack by the dominant animal.

II. Agonistic Behaviour

(a) An Attack

This consisted in (i) grasping, and (ii) if the animal pressed the attack, biting the opponent. Females off heat usually only grasped hold of the animals; on heat they appeared to bite also. Most bites were on the back of the head and shoulders. This behaviour was often preceded by a chase, the fleeing animal being caught. No combat fighting (effort-ranking—see Chance & Mead, 1952) has yet been observed between any two animals. (The attacks of the overlord (D1) were infrequent, but were delivered with full force. This means that he chased one animal persistently, and after digging his teeth into the victim, held on; sometimes for as long as a minute).

(b) Threat

This assumed increasing degrees of intensity, as the following acts were added to each other: (i) looking directly at the opponent, (ii) raising the ears (to different extents), (iii) thrusting the head forward on the neck and lowering it sharply, (iv) raising the body on all four rigid legs, with back straight, (v) jerking the body down and up sharply by flexion of all four legs simultaneously, (vi) raising hair on back, (vii) advancing and stopping, and (viii) chasing.

The mouth was frequently pouted during threat, but this gesture also occurred in conjunction with other facial gestures when an adult male encountered an adult female accidentally. Its significance remains in doubt.

(c) Equilibratory Behaviour

Equilibratory behaviour includes those acts which a monkey may perform in response to potential or overt threat. It lies in between, but does not include, attack and flight.

Forms of Equilibration

(a) Spatial equilibration. The simplest and most frequent form of equilibration was an adjustment of the spatial relations between the threatened animal and the source of the threat, or potential threat; usually the animal moved off a short distance, and remained facing the potential aggressor, e.g. in response to the movement of an animal higher in the dominance hierarchy. This was the response of at least half the animals in the colony at any one time to the movement of the males or females of the breeding hierarchy. The response was more marked to the movement of animals high in

order of rank. In its least obtrusive form the animal would get up and walk away to another spot after taking a glance in the direction of a dominant animal on the move, or in response to an animal which walked directly towards it without obvious threat. If accompanied by counter threat, the animal might move towards the threatening animal. Adjustment of spatial position entered into all other forms of equilibration.

(b) Postural equilibration. *Submissive gestures.* These replaced movement away from the aggressor and also facilitated approach under threat.

1. Crouching. This consists of lowering the body to the ground and clutching on to the rock. The animal frequently combined this posture with crawling up to and lying in front of the potential aggressor. The Eech sound might be emitted and the ears were drawn back.

2. Presenting. This is the female copulatory stance and consists of directing the hind quarters towards a potential aggressor. In a fully developed form the fore-quarters are simultaneously lowered. (The animal to which the presentation has been made may mount, i.e., by grasping the hocks with the hind feet and the middle of the back with the fore-feet, and executing pelvic thrusts slowly. This frequently ends the relation of the two animals).

(c) Oppositional gestures—various degrees of counter-threat.

(d) An asocial gesture. A neutral gesture consisting of folding the arms and legs close to the body and lying or crouching bunched up on the ground. This appeared very suddenly in agonistic situations and lasted only a few seconds. It seemed to remove the animal temporarily from the social environment during periods of intense and complex social activity. Other animals took no notice of an animal in this position during the excitement of the moment, though afterwards it was recognised and investigated.

Adult types of equilibratory behaviour. Both male and female adult animals of the breeding hierarchy characteristically combine threat and submissive gestures in approaching a more dominant animal, especially the overlord. This behaviour consists of simultaneous threat towards an animal in the vicinity, outside the social space, with presentation towards the overlord and short bouts of backward movement towards him. In the backward approach of a submissive towards a more dominant monkey, the submissive monkey adopts the posture indistinguishable from that of the female consort of an adult male during the initiation of the ritualised mating sequences which so often appeared in the behaviour of the overlord and his consort. Yet used as a method of guarded and gradual approach, it is alternated with short bouts of backward movement towards the dominant animal, at the same time looking towards him. This behaviour is not very often followed by a copulatory sequence when the animals come close together. The term "sign-equilibration" will be used to denote the postural elements present in approach or avoidance and is typical of the behaviour of D3 and the anoestrus females to the overlord. The body posture is adjusted by various degrees of presentation to a suitably submissive attitude which is then combined with gradual approach. Characteristically, the animal presents with its hind quarters and, continuing to keep the dominant animal in view, moves with frequently arrested step at an oblique angle round the dominant animal to a position which is finally closer than that from which it started. The oblique path may be converted into a zigzag, in which the movements towards the dominant animal are greater than those away from it. This is done by threatening and advancing towards a third animal for which movements away from the dominant animal are required. Subsequently, having aroused the dominant animal to awareness of this threatening behaviour directed at another animal, the subject backs and presents towards the dominant animal.

All these, and the vocal calls Eech or Hough-Hough, are combined in various ways and in different degrees of intensity and frequency to produce a complex pattern of social relations. As an example, an animal may stand and look alternately towards and away from the threatening animal, gradually moving away from or towards the threatening animal in short bouts of movement, ears alternately drawn back and directed forward, and emitting the Eech sound.

(e) Fleeing. The animal ran on all fours as fast as possible, and only occasionally looked backwards.

III. Display of Dominance

From time to time a medium sized or adult animal would run about, seize the branches of the tree trunk and with quick extension and

flexion of the legs jerk up and down on a branch. During this behaviour the animal would often move up to the top in little leaps. When at the top the animal would remain in some prominent position, either walking about with a rigid body posture and stiff legs would look down at the rest of the colony, or would hold on to or sit on top of the branch. Adult females preceded this type of behaviour by darting about and standing in prominent positions occasionally threatening in all directions, emphasising the threat with sudden jerky lowering of body on bended legs. The adult males, on the other hand, never used this gesture, but preceded the mounting of the log which leant against the hill by roaming the colony individually, or as a group, often running at a gallop before mounting the log.

IV. Copulatory Behaviour

Pelvic thrusts frequently, though not invariably, followed mounting. In many instances, however, the presence or absence of pelvic thrusts clearly had little significance, since in these circumstances it appeared to be an affinitive gesture establishing recognition of relative, if temporary, dominance status between the two animals. In this form copulatory gestures were part of agonistic behaviour.

(1) Pseudo-Copulatory Behaviour

This term is applied to the instances recorded in which the tip of the tail of the mounting monkey was applied to the ano-genital region of the presenting monkey. This occurred in many instances of the behaviour of medium-sized and some young monkeys. It may be restricted to the behaviour of immature females, but the sex of the animals was not observed.

(2) Copulation

Evidence in the form of vaginal out-flow of semen was only definitely observed once, but the behaviour of adult males and their consort females frequently took on a ritual copulatory sequence in that many pelvic thrusts followed the mounting. Threat on the part of either animal is then immediately followed by threat in the same direction by the partner. Typically, when close to the male, the female, after threatening away from the male, threw her body across in front of him, moving the hind feet up and down sharply in short bursts as she brought her hind quarters towards the male, or if she were far away, her threatening behaviour was followed by a presentation stance, and he moved over to her and copulation took place. This was frequently repeated and both animals appeared to be in the grip of a ritualised sequence of acts forming a "reaction chain." This behaviour always developed whenever the female or the male threatened a third party, or threatened apparently indiscriminately in a direction away from the partner.

V. Play

This included: (1) grasping of one animal by another, (2) attempts to bite, (3) pulling, in attempts to displace or turn over, (4) rolling over, (5) jumping: (*a*) in the air by itself, (*b*) and catching at tail or grasping, (*c*) and looking through its legs, (*d*) losing its balance (repeatedly) (6) sliding off tree trunks, etc., (7) imitative, incomplete activities: (*a*) pelvic movements, (*b*) threats, (*c*) equilibratory movements and gestures, (*d*) biting.

VI. Bathing (Juveniles)

(1) Jumping into water, (2) walking slowly into water keeping tail and head out, (3) swimming under water—dog paddling, (4) swimming on surface.

VII. Grooming

(1) Picking over fur of other animal, (2) picking over fur of self, (3) examining own body.

VIII. Erotic

(1) Playing with genitals of self (or other animals), (2) erections in male (during lying out on hot days and while being groomed).

IX. Running

Relaxed trot runs without obvious directed effort.

X. Huddling

Huddling into groups was more frequent when cold, but was apparent at times when not sufficiently hot to disperse sleeping animals singly or into grooming pairs. This behaviour may provide a means of sleep by ensuring some degree of protection against the need to equilibrate. Small groups have been observed to break up and often one or two animals will leap out of the centre or away from the edge. This sudden disturbance is often accompanied by Eech sounds and suggests that aggressive behaviour emerges during relaxed behaviour as well as during activity.

XI. Social Space

Social space arose out of the spatial equilibration of subordinate animals towards the

dominant members of the colony. The changing social relations within the colony were responsible for the fact that during the first two months only female and young were excluded from the space surrounding the overlord. Later, D2 occupied positions at the edge and the females, except at the peak of heat when they became the overlord's consort, remained on the edge.

THE COLONY

The Dominant Set

Soon after the introduction of the animals, it became possible to identify most adult animals both by their appearance and by their behaviour. Three features made it possible to distinguish early on the leading members of this colony.

(1) It was possible to distinguish three adult males, D1, D2 and D3 in order of rank, who were constantly together in a group and often roamed with each other. These three males are referred to collectively as the dominant set.

(2) Moreover, they were almost always as a group, and often as individuals, surrounded all the time by a space which separated them from other animals.

(3) Their posture when seated or in movement was noticeably relaxed. The overlord (D1) had features which in many respects were distinctive. His body contour was more muscular and sharply defined, partly because the hair which ran into ridges added modelling to the surface of the body. The hair was also well groomed and glossy. The overlord could be distinguished at all times by his relaxed postures. Whenever he sat down without accompanying activities, such as feeding or grooming, he adopted a characteristic posture consisting of partially extended hind limbs, curved back, drooped head, and forelimbs resting on the ground. Sometimes his fore limbs were extended towards his feet. He frequently lay down. His movements were those of a lope rather than a walk. He was rarely, if ever, associated closely to the extent of contact with other animals, except his male consorts, D2 and D3. On one occasion, however, on 29th May, he was seen to play with a young male for about a minute. This was, however, a very surprising observation in view of his earlier behaviour, and remained an isolated example throughout the whole period of observation.

The second in rank was a stouter animal with the same characteristics as D1 to a less marked degree.

Finally, the male ranking third possessed the same well groomed appearance, and adopted the same relaxed posture with his legs and forearms. He could be distinguished from the other two by being much darker and holding his head in a characteristic position, lowered and often bent backwards.

Cycle of Activity

To some extent this depended on the availability of food, but, while the animals were only fed once a day, the afternoon siesta of the dominant set was the most constant feature of their behaviour, often taking place on a preferred ledge on the southern face of the west hill.

Roaming of D1 and Threat by Members of the Dominant Set

The dominant male from time to time set out on a tour of the colony, loping or bounding from ledge to ledge or galloping along the flat terraces, dispersing large numbers of the animals who either fled or equilibrated. He was often accompanied by D2 and D3. Suddenly D1 would focus attention on a particular animal and chase it until he had caught it or it had disappeared round some prominence. If he caught it he gave it a severe mauling. These violent assaults were typical of D1.

D2 showed running threats typical of, but less intense than, D1; e.g. D2 only once seized an animal by the tail but did not press the attack when the animal escaped. These sudden and rapid approaches were typical of both animals. It was of interest that while in a sleeping group or a resting group, D2 twice broke away to chase off small animals which were playing in the vicinity. This was unlike D1. Eech sounds did not arouse either animal. D1 did *not* use Houghs, but D2 did.

The Females

Many of the adult females were long and thin in the body; one was plump, and the rest were small. Their fur was always less well kept than that of the adult males.

Clusters of Small Animals

Except when the weather was very hot and all the animals of the colony were dispersed in ones or twos, the young and medium sized animals rested in groups consisting usually of more than half a dozen animals. Although the majority

of the animals in these groups were resting, many were grooming or asleep.

Carpenter (private communication) states that "clusters of early and late juveniles form groups which may persist for a long period of time." It is possible, therefore, that the grouping observed amongst the young animals of this captive colony was an expression of a tendency observed in the Santiago Colony inhabiting wooded country.

The Social Structure of the Colony

This falls into two periods: (1) the period of the dominant set when none of the females had yet come into oestrus and (2) the period of the breeding hierarchy established by the advent of oestrus cycles in at least one female. Throughout the period the number of adult males remained constant as judged by the fact that no new males entered the breeding hierarchy, but the number of separate females with oestrus cycles increased from one to ten from June until November. At the start, the number of animals in the colony declined rapidly from a variety of causes, but after about 6-8 weeks the deaths from tuberculosis were about 6-8 per month. At the end of the present study about 110 remained out of 253 liberated on April 3rd. With the exception of one adult female, the loss occurred exclusively amongst middle and small sized animals.

The Period of the Dominant Set. April 3rd—1st week of June

The affinity of members of the dominant set for one another was evident from their close proximity at most times. They slept, huddled and relaxed next to each other, groomed each other, presented to and mounted each other, fed in close proximity to one another, occasionally took food from one another and even ate out of each other's hands, although D2 and D3 were sometimes separated from D1, the overlord.

Yet equally clear was the distinction between them. Each made it obvious that pride of place or dominance belonged to one of them, and that D2 ranked higher than D3. Dominance is usually defined as priority of access to a need satisfying object, but, since in this instance, no priority of feeding was shown, it was in the relations of the animals to each other that the order of rank was made manifest. At all times D1 was relaxed in approaching the others, though on occasions he presented to his colleagues. This was with as much ease of movement as with any other gesture. At no time were his movements jerky. In contrast, D3 approached D1 either by sign equilibration or by crawling gradually, and by stages, closer, or he would equilibrate and present at the approach of D1. D2 was less likely to move on the approach of D1, but he did not fully relax until D1 was himself relaxed; he approached D3 always with a relaxed gait.

The obverse aspect of their behaviour was the relative absence of threat between the members of the set. In this feature the behaviour of this group was distinguished from that of the rest of the animals of the colony. The dominant male had not yet been seen to threaten either of his subordinate colleagues. On the other hand, D2 occasionally exerted mild threat towards D3. D3 had responded on occasions by moving to a greater distance. It appeared that D3 may have had a somewhat insecure position within the set, since during grooming by D1 the position of this animal was not as relaxed as D1 or even as D2. Moreover, the prominent place occupied by sign equilibration in the approaches of D3 to D1 also emphasised this instability.

It was characteristic of the dominant set that they enjoyed social mobility, i.e., freedom of movement within the colony, both as individuals and as a group. Associated with this freedom of movement, social space arose within their vicinity whenever they moved towards, or close to, a group of animals. This means that an area formed around them in which there were no other animals. This area appeared to have a radius of approximately three to four feet. The movement of other animals away from them did not arise as the result of active flight from the approach of the dominant set, but rather that after settling into a locality, no subordinate animal entered the space in their vicinity and animals already there gradually and quietly moved away.

The Behaviour of the Adult Female during the Period of the Dominant Set

There were also three adult females which were amongst the largest animals in the colony, although they were probably not as heavy as the dominant male for they were very thin. The behaviour of the females was similar to each other in every respect. One of the females appeared to have entered an oestrus phase between the 20th and 30th of May. The early reddening of the sexual skin in this female was followed by a sexual swelling which was on the decline on the 31st of May. This female passed

through a full oestrus cycle. The other two females were noted on the 23rd of May to be entering the oestrus phase by the more intense red colour of their perianal skin, though they were not seen to have sexual swelling.

The three adult females were amongst the most mobile of all the animals. They were frequently roaming round the colony, threatening animals in their vicinity, but social space did not invariably form around them. They rarely seemed to play, but were amongst the most active animals on the logs. Despite their frequent threats, they had close association with a number of animals of all sizes, grooming and huddling with them. They frequently grasped small animals by the tail or a limb, and drew them close towards them. The females were apparently more aggressive, and when their sexual skin was a more intense red frequently chased a number of animals throughout the colony. On one occasion, one of the females in the early part of oestrus systematically cleared the animals which were bathing from around the pool, and kept them away for several minutes at a time.

Occasionally in the anoestrus phase, and more frequently during oestrus, the females grouped themselves round the dominant animal D1 after he had moved away from his male consorts. When he was seated alone, the females took up positions about two or three feet away, continually looking towards him and away from him. Such activity was accompanied by threats and counter-threats between the females. On one occasion, the threatening female came into such a position that simultaneously she presented to the dominant male, and was mounted for a brief interval; copulation did not occur. On one other occasion, the dominant male was seen to mount one of the females, but this time her presentation was unaccompanied by threats towards the other animals. The behaviour of the dominant animal during the greater part of these inter-female equilibratory activities was one of immobility, and apparent disinterest. It was always his movements away from the scene which broke up the setting for this kind of behaviour. Occasionally, females entered into equilibratory movements around the dominant set on the preferred ledge during the afternoon siesta.

The Emergence of the Breeding Hierarchy

Some time after 31st May and before the 7th of June, a change took place in the relation between the three dominant males. On the 7th of June the appearance of D1 had changed; he was lacerated on the shoulder and his fur was dishevelled. From these signs it would appear that he had been involved in a fight. What the nature of the conflict was is not known as it was not possible to identify an opponent. Suffice it to note that, whereas on the 31st of May all three males roamed the colony together, after the 7th of June these three males were closely associated only for brief intervals during short periods when the females were in anoestrus. On these occasions D1 and D2 sometimes came together for very brief periods of grooming. The position of D3, however, which until now had been similar to that of D2 soon changed. Within a month he was seen in the company of medium sized males and later associated exclusively with younger animals, except for occasions when he would move unmolested through the social space round D1, D2 or both when they were close together. In this respect his relations with the dominant set seemed to have become almost neutral. This separation coincided with the advent of oestrus in at least one of the females, for shortly after the separation, D1 was consorting with a female on heat, and shortly afterwards D2 also had a consort.

Here, therefore, in the evolution of these social relations, we have evidence similar to that found by Zuckerman (1932) in his study of Baboons in the same enclosure. He says: "It is perhaps interesting to note that when all females were removed from the Hill the abandoned overlords immediately merged with the group of bachelors. An observer with no previous experience of the colony would be unable to pick them out."

In fact, the course of events which has emerged in the present study has provided us with a corroborative set of observations if we assume that the social relations in the two species of cercopethecid monkey are essentially similar.

In this connection perhaps the fate of D3 has placed him in a peculiar situation forced on him by the absence of a bachelor group to which to retire. On the other hand, the observed changes in his behaviour suggest that a regression to infantile behaviour had taken place, since he now joined the clusters of young animals and played with young.

Relations within the Breeding Hierarchy

Carpenter (1942) makes clear in his descrip-

tion of the colony of Macaques in the Santiago Island Colony, that the females on heat enter into association with males of the breeding hierarchy. In his description, six or eight males were present in the breeding hierarchy; the females associated first with low ranking males and finally, at the peak of oestrus, with the dominant animal. Observation during one month revealed that the pro-oestrus and oestrus females consorted with D1 *first*, and that following the peak of oestrus they moved on to D2 for a few days. This relation was established by active threats of the females towards D1 and to a lesser degree towards D2.

In the early days in the latter half of June, the adult males were, however, never close together. D1 and D2 were now both in association with females and occasionally separated from them as a diversion of attention took them different ways. The consorts soon rejoined each other and remained close, and either rested or behaved to each other in the typical copulatory sequence for the female supported by the male.

Later, this marked and persistent separation of the males and their close association with one female was replaced by a more fluctuating relationship both between D1 and D2 and between each of them and the adult females of which there were, by the end of August, some five or six in different stages of the cycle. Despite the fluctuation which depended on the relative stages of the cycle occupied by different females, certain elements of their behaviour were always present.

D1 and D2 were now separated when at rest or asleep by a small, but definite distance which at all times was hardly less than three feet, and which extended to about twelve feet following, or during, periods of much social activity.

DISCUSSION

Role of Mating Gestures and the Occurrence of Copulation

Carpenter (1942) makes it clear that presentation and mounting only constitute a stage in the mating behaviour when a male follows the mounting of a female by several rapid pelvic thrusts. Copulation is completed only when a series of such mountings is terminated by ejaculation.

Presentation takes place often without the animal being mounted. Carpenter makes it clear that it is likely to appear in the behaviour of excited females in a variety of situations and has different functions, e.g. as a greeting gesture, as an expression of affinity or as part of what is called here "sign equilibration"; when combined with outwardly directed threat it serves to redirect the aggression of a more dominant animal. Finally, it appears to diminish threat especially when combined with facial gestures directed towards a more dominant animal, and may in this way provoke mounting by the dominant animal in place of an aggressive approach.

The mounting of one animal by another, preceded or not by presentation on the part of the subordinate animal, is a part of the social relations between all ages and sexes alike. In the behaviour of adults the act is usually followed by about half a dozen quick, vigorous pelvic thrusts. In the young the thrusts are less vigorous, and the behaviour less definite. Adult males mounting do so with the penis erect. In middle sized animals the tail has, on about half the observed occasions, been used to prod the rump of the mounted monkey. It is almost certain that the majority of the mating gestures exhibited so frequently between these monkeys serve at least one function which is non-reproductive and non-sexual. It expresses the acceptance of dominant and subordinate status between two animals, as for example when, towards the end of play in medium sized monkeys, the one monkey mounts the other after his playmate has presented to him. The play then ends. An alternative hypothesis is, however, possible, namely, that this is a structural form of contact which expresses affinity between two active animals, just as huddling and grooming does in a quieter state of excitement. This appears likely since mounting of one animal by another may be immediately followed by the same behaviour with the roles reversed.

Analysis of the Social Relations within the Breeding Heirarchy

1. A strong male attraction existed between the males, amounting to a definite male society. The characteristic social behaviour of the society made it clear that it is both (*a*) affinitive and (*b*) hierarchical.

2. In contrast, we have no observation which suggests that there is a comparable relation between adult females at any stage of the cycle, but as far as could be ascertained each anoestrus female lived a life independent of other females,

associating as much with young as with other adult females.

3. The advent of the first oestrus cycle in one of the females changed the relation of the males to each other, and to the females. This change was manifest in the following ways:

(1) The dominant male was involved in a fight on one occasion, the nature of which was not observed.

(2) The males separated. D2 then observed the social space around D1 to a degree dependent partly at least on the number and behaviour of (*a*) the females on heat and (*b*) those which had been on heat.

(3) D3 was displaced altogether from the breeding hierarchy. He associated more and more with young animals exclusively, was docile and played with them.

The way the change came about will remain obscure, but some idea of what may have occurred can be surmised from the relationships within the breeding hierarchy which came into being at this moment.

(4) Females coming on to heat actively forced their way into association with the overlord male by threatening him and actually chasing him. He did not in any way relatiate, but on occasions retreated from these advances.

Analysed in terms of the agonistic components of approach-avoidance conflict the records provide evidence of the following features.

Affinitive Relations

(a) Mutual

1. Attraction was mutual between the adult males during the time they constituted the dominant set and remained between those which entered the breeding hierarchy, i.e., D1 and D2. The relation of these two animals was characterised by mutual grooming, mounting and being mounted. They remained in the neighbourhood of each other whenever the activiy of the females was in abeyance during anoestrus.

2. Attraction existed between the male and his consort as was shown in the same way.

3. D2 was attracted to the first consort female during September, since he frequently moved near her whenever she separated from the overlord, and her behaviour in accepting a mounting if D1 was away does give some evidence of a reciprocated attraction.

(b) Uni-lateral

1. It is difficult to assess the behaviour of the pro-oestrus female who directs her attention more and more towards D1 since her approaches were always accompanied by threats. Her attention to D1 however, suggests that at this stage of the cycle she was attracted towards him. Since he ran away he was, as yet, not attracted towards her. Later, however, his behaviour led him to mount her more and more often until finally they were so closely attracted toward one another that she, at times, mounted him.

Thus, it would appear that threat itself engenders attraction of the male towards the female, and in this particular relation a threat might be termed an erotic stimulus. However, there is an alternative interpretation which is more generally applicable since we must first complete the picture by including the oppositional relations.

Oppositional Relations

These are revealed by the existence of threat from one animal to another, and the awareness of dominance or potential threat by spatial or sign equilibratory movements.

(a) Mutual

Between adult females.

(b) Uni-lateral

1. The existence of potential threat down the adult male hierarchy is revealed in the second manner.

2. (*a*) This is emphasised by a redirected aggression from D1 to D2 when D1 is under threat from a pro-oestrus female; (*b*) when D2 approaches too close to D1's consort female he is threatened by D1; (*c*) when D1 supports his consort female in threat towards other animals.

3. As dominance displays, i.e. shaking log, standing in prominent positions, and threatening in many directions in rapid succession.

The inter-action of these categories of conflicting influences leads to a balance of attractive and repellent forces between the animals in a way illustrated by Figure 1. This figure not only indicates threat and attraction between animals, but also depicts the resulting spatial relations as observed during the different phases.

Three significant omissions appear, namely, (1) complete absence of attraction between the females since these do not consort together in anoestrus; (2) complete absence of threat from

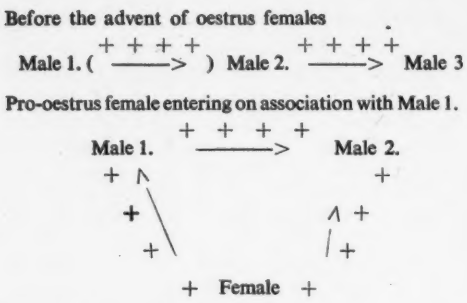

Fig. 1. Diagram of the relations between the adults and the resulting spatial configuration.

D2 to D1, i.e. up the hierarchy; (3) only few and weak examples of threat from males to females.

This last point is especially significant since in the single instance when D1 rushed at a female he stopped short suddenly and moved off in another direction, suggesting that the females possess a sign suppressor of threat, the nature of which has not been identified.

The Constancy of the Affinitive Relations between Adult Males of the Breeding Hierarchy

The prominence of the mating relations in the social life of primates has led those who previously worked in this field to see in the attraction between the sexes the primary bonds uniting the individuals into a group or society. Against this, however, must be placed the fact that in other animals which come into oestrus all the year round, the members of a breeding pair are not found necessarily associating with other pairs. Moreover, other animals, such as wolves and deer for example, form constant associations outside the breeding season and the wolf society breaks up into pairs for breeding. It is, therefore, possible that another bond which is not primarily of a sexual nature constitutes the fundamental link in the chain of relations forming the macaque society.

It should be noted that Zuckerman (1932), describing the social unit or family group of the baboon colony on Monkey Hill, drew attention to the possibility that the attached bachelors may be attracted by the overlord: "A family group consists of a male overlord, his female or females, together with their young, and may sometimes include one 'or more 'bachelors' or unmated males. The bachelors are not an essential element in the party, although they may be attached to it, according to my observations, for as long as a year. As is explained below, they appear to be held to the group mainly by their interests in the females, *but it is possible that they are also attracted by the overlord.*"

Several features of the adult male macaque's behaviour in the colony suggest that the attraction between them is certainly the most permanent force uniting the members of the breeding hierarchy. Not only were the three males, united before the females coming into heat forced their way into association with the males but also the cohesion of the bonds uniting D1 and D2 is certainly manifest by the fact that it re-asserted itself in the behaviour of these two animals even in the presence of the adult females, provided that two females were not close to the peak of oestrus at the same time. Even in these circumstances, although the males were widely separated, the movement of one was constantly attracting the movement of the other. Moreover, the adult females in their behaviour to one another provide a contrast which is almost certainly as significant as it is striking, for they do not form any constant associations among themselves. The most obvious part of their mutual relations is the constant threat which passes between them on the edge of the social space, and this serves to emphasise perhaps that the influence holding them together into the society is their attraction for the males.

It now becomes clear that the most permanent bond of this society was the relationship between D1 and D2 and that the temporary association of the mating relations was grafted on to this. We may now enquire what is the nature of the attraction holding the adult males together, and the first point to note about their behaviour is that during the period of the dominant set an order of rank existed between them. This may mean that the subordinate members recognise a potential threat from those superior to them. Such a sign of potential threat in the behaviour of the overlord would inevitably serve to separate the animals as widely as possible, if it were not simultaneously balanced by an equally strong attraction. In this relationship, therefore, the essential features of equilibratory behaviour are manifest, and since the attraction is not primarily of a sexual nature the most fundamental bond creating the society of this monkey appears to be a male characteristic and is an integral part of the mechanism underlying dominance.

Comparison with Carpenter (see next section) shows that despite many differences in the behaviour of members of the breeding hierarchy towards one another in the different colonies, existence of a permanent hierarchy is a common feature and is evidence that it is fundamental to a macaque society. It can be inferred that if any high ranking member of the male hierarchy moves his position to an appreciable extent away from the others then they will follow him. Carpenter (private communication) reports that if the overlord wanders far afield in pursuit of his consort female, the whole society follows.

The ultimate attraction of the male for the oestrus females is the sequel to her aggressive behaviour. The consort relationship, therefore, has its origin in a situation very similar to the relations between D1 and D2 if we assume that the relationship was established in the first instance by the attraction of D2 for D1 and that the reciprocal attraction was acquired by D1 through familiarisation. Both the attraction of D2 for D1 and the attraction of a male for a female exist closely associated with an oppositional component which exists either contemporaneously with it or precedes it. Presumbly, therefore, threat may (as a result of repeated visits) be a means of evoking attraction in a male Macaque as well as acting to repel another animal. Clearly, males and females behave very differently in response to threat.

Comparison with Earlier Studies

While it is possible to be doubtful about conclusions drawn from the intermittent study of social behaviour in a colony, as in this instance, this criticism also applies to all previous studies. Comparison, therefore, between this and similar studies is legitimate if the limitations are borne in mind. The following analysis is made, therefore, in order to facilitate enquiries into the earlier studies of Carpenter (1942a and b) and Zuckerman (1932). It is worth noting that in several important respects the behaviour of the animals of the breeding hierarchy differed from that reported by Carpenter for Macaques in the Santiago Island Colony. The most notable difference is the high level of attacks as well as threats by females on females. Thus, the females behaved towards each other in essentially the same way in both colonies, but the intensity of opposition between the females was increased by attacks as well as threats on Santiago Island.

A high degree of opposition is also present in the behaviour of the males towards the females coming into oestrus, which were subject both to attacks and "bluffing attacks" by the males of the breeding hierarchy on Santiago Island. This appeared also in the behaviour of the overlord to his consort, and may have been a consequence of the behaviour of some females which changed their consorts several times during oestrus. The high level of oppositional elements is itself evidence of a high level of conflict. This may be the essential difference between the two societies.

A further notable difference was the prominence of facial gestures in the approach of females to the males of the Santiago Colony. In both colonies aggressive behaviour was part of the oestrus females' behaviour, but Carpenter's description does not include specific mention of threats by females towards the males they solicited.

These differences are sufficiently great to suggest that they reflect the response of the individuals to the very different conditions of the two colonies. This cannot be a reflection of a difference in density of the two populations due to a difference in territorial confinement, since in the Santiago Colony, showing the higher level of social tension, the territory of the group was much larger than the space

available to the monkeys of the colony on Monkey Hill. Should this prove to be so, as is also suggested by the altered social structure in the changed condition of the Colorado Island colony of Howler monkeys on the occasion of the studies of Carpenter during 1932-33, and that of Collins & Southwich (1951) it may well reveal a flexibility in the individual control of social responses which in each set of circumstances leads to the establishment of an appropriate social structure. This may then acquire some degree of stability as a result of learning on the part of subordinate animals.

The Relation between the Adults at Different Times

The foregoing analysis provides the means of identifying the separate elements in the relation between adults, and these are expressed in a diagrammatic form in Fig. 1. Here, bonds of affinity are expressed by a set of four plus signs and the relative strength of oppositional behaviour by the length of the arrow. Relative spatial configurations accompanying the interaction of these two opposing factors are also shown. This brings out the fact that the animals behave as if the attraction between males and males, and males and females is a factor of constant strength and that the distance separating adult animals is, therefore, a reflection of the strength of the oppositional forces.

Stress

It has been a frequent comment that the conditions on Monkey Hill were "abnormal." It should be remembered, however, that this could equally well be said of the earlier studies mentioned here, since in each instance the monkeys had been "liberated" into new surroundings for the purpose of study. What is important is that the conditions should be clearly described for comparison with other studies, whether in a natural or an artificial environment. Such comparison may then reveal the constant and variable features of the society. Elsewhere, (Chance, unpublished) an attempt has been made to evaluate stress quantitatively, as a simple measure of the intensity of conflict engendered by agonistic social behaviour. Suffice it to say at this stage that the colony on Monkey Hill was under considerable stress from a variety of non-social factors. Notable amongst these were: (1) the after-effects of the journey during transport from India to this country, (2) the high incidence of different types of dystentery, despite measures adopted to rid the colony of this disease, (3) infection from tuberculosis.

A high death-rate, mostly amongst the young, averaging 12 per month during the period of the study, could not be accounted for solely as a result of these factors, as 4 animals died with full cheek pouches and no pathology on post-mortem examination. Such deaths may possibly be the result of fright during agonistic social encounters. If so, this could also be a contributory factor in the etiology of the infections.

SUMMARY

1. Various methods of observation were tried in order to obtain accurate records of individual behaviour in a social environment. Observing one individual for about an hour and recording the behaviour every two minutes was found to be the most practicable and reliable procedure.

2. A list of the different acts of this monkey is given and the component elements of the equilibratory response in agonistic situations are recorded.

3. The main social features and the changes with times are described. A close affinity and an order of rank between the only three adult males is described and it is pointed out that, as reflected in the behaviour of the two top ranking males, the affinity remains unaltered even with the advent of oestrus in a number of females (ultimately ten in number). The third in the hierarchy behaved differently as a result of the change in the behaviour of the adult females. His behaviour regressed to a more infantile type.

4. The persistent affinity of the males for each other contrasts strikingly with that of the adult females which possess no constant association. It is suggested that the bond between the adult males is *per se* an adequate foundation for the sociability of these monkeys enabling the breeding pairs to remain together when sexual conflict is aroused by the simultaneous presence of more than one oestrus female.

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from day to day. I wish also to thank Gabriel Horn for undertaking the continuous observation of the colony for one month, by which means many important features of the adult behaviour were clarified, and Nöel and Frank McGuiness for their valuable assistance.

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THE BEHAVIOUR OF HONEYBEES PREPARING TO SWARM

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Introduction

Probably the most extensive description of the entire process of swarming is by Huber (1792). Taranov & Ivanova (1946) made similar observations, but in their account no dates are given, and so it is difficult to obtain a comprehensive picture of the sequence of events; many details, including notably those of the behaviour of the bees immediately before the swarm issues, are also omitted.

The present paper, giving a detailed account of the events which occurred in a colony from the time when the first queen cup was formed until after the final cast had departed, fills in some of the gaps in knowledge and corrects certain misapprehensions.

Method

A small colony of bees was kept in an observation hive containing three British Standard Brood frames arranged vertically above one another. They could fly freely by way of a hole in the base, communicating with the exterior via a glass-covered channel about a foot long.

Estimations of numbers of bees were made visually, using the method described by Jeffree (1951). Approximately 4,500 bees, with a year-old, clipped and marked queen, were present in the hive at the start of the observations on 18th May, 1954. Observations were continued until 2nd August, 1954. For purposes of identification, the queen cups were numbered in order of formation.

Events Preceding the Issue of a Swarm

1. Queen Cell Formation

The earliest signs of any preparations for swarming were seen on 28th May, with the formation of a queen cup. No more cups were seen until 9th June; this one was the first of seventeen which were built at the rate of one or two every few days until 14th July, after which no more were formed (see Table I). Not all these cups were used to rear queens—only seven reached the stage of being sealed, and out of these only four virgins emerged. A prime swarm left, with the old queen, on 7th July, and five days later the first virgin emerged from a cell which had been sealed for eleven days.

Two of the sealed cells which did not hatch were torn down shortly after the final cast left on 19th July, while the remaining one was opened by the bees a few days after sealing, and the body of a dead queen removed.

It is almost certain that on some occasions the eggs or larvae in the queen cells either died or were destroyed, because at different times several drawn-out queen cells were cut down to cups again; moreover, the queen was seen to lay twice in each of two queen cells. One of these two cells was not enlarged to any extent, and another in which the queen was seen to lay also showed no enlargement.

Bad weather conditions during the swarming period may delay or even prevent swarming (Huber, 1792; Alfonsus, 1932), and it is possible that the number of queen cells cut down in the present instance were a consequence of the conspicuously cold and wet weather prevailing throughout the summer.

2. Behaviour of the Workers

In the pre-swarming period there was a progressive reduction in the number of bees supplying the queen with food. This number fell to a minimum in the fortnight before the queen left with the swarm, when hardly any bees fed her. In spite of this she continued to lay a small number of eggs each day up to and including the day of swarming. Table II gives details of the number of times she received food during one-hour periods on selected dates and also the number of eggs laid during these periods. The first persistent refusals to supply food were noted on 31st May, three days after the formation of the first queen cup, and by the 15th June these refusals had become more frequent. However, after this state of affairs had continued for a few more days, the queen was soliciting food on fewer occasions than previously. Taranov & Ivanova (1946) stated that in the pre-swarming period attendants repeatedly tried to force the queen to accept food, but this was definitely not the case here, although the queen did refuse food from a few attendants at widely separated intervals.

It has been shown (Allen, 1955) that the age of bees feeding the queen in this colony between

Table I. Details of Queen Cells

Queen cell No.	Date of commencement	Date of sealing	Date of hatching	Notes.
1	May 28	—	—	—
2	June 9	July 1	July 12	1st virgin
3	June 10	July 4	—	Cut down by bees after departure of final cast.
4	June 14	June 26	—	Dead queen removed by bees on July 4th.
5	June 19	July 2	July 13	2nd virgin
6	June 21	July 4	July 19	3rd virgin
7	June 21	—	—	—
8	June 28	July 4	July 19	4th virgin
9	June 28	—	—	—
10	June 28	July 4	—	Cut down by bees after departure of final cast.
11	July 2	—	—	—
12	July 5	—	—	—
13	July 7	—	—	—
14	July 7	—	—	—
15	July 11	—	—	—
16	July 11	—	—	—
17	July 12	—	—	—
18	July 14	—	—	—

27th May and 9th June was significantly higher than that of bees feeding her between 10th and 21st June. This difference was considered to be related to the swarming impulse, which began in earnest on 9th June with the building of the first of a fairly rapid succession of queen cups. No bees older than six days were seen to feed her in this second period, as compared with a maximum age of eleven days in the first.

Taranov & Ivanova (1946), from observations on a colony with queen cups, described a process (which had been mentioned by Huber, 1792) in which the queen was shaken at intervals by workers quivering on her; they regarded this as a normal occurrence in a colony preparing to swarm. Istomina-Tzvetkova (1953) described a similar event taking place between workers, but she did not connect it with swarming, although her observations were carried out during the summer. She stated that one bee would jump continually on the backs of others and quiver on them, and records that in one case a single worker jumped on 84 other workers during one day.

In my colony both the queen and the workers were sometimes shaken. Moreover, it did seem that the shaking of the queen, at any rate, bore some relation to swarming, since it was first observed on 8th June, when swarming preparations were about to begin in earnest, and it became more and more frequent until it was almost continuous by 16th June. From this date until the bees swarmed there were, at most, only pauses of half a minute in the succession of workers shaking the queen. In the period between the departures of the prime swarm and

Table II. Egg-Production and Feeding of Queen

Date	No. of eggs laid in 1 hour period	No. of feeds in 1 hour period
May 26	17†	7.0†
„ 27	17†	6.0†
„ 28	22†	3.5†
„ 31	37	4
June 8	18	4
„ 11	16	3
„ 16	16	0
„ 17	17	2
June 21	22	0
„ 22	12	0
„ 23	27	0
„ 28	16	0
July 3	11	0
„ 4	7	0
„ 6	11	0
„ 7(1)	13*	0*
(2)	3*	0*

† Mean of 2 periods.
* (1) 8.55—9.55 a.m. G.M.T.
(2) 2.10—3.10 p.m. G.M.T.
The swarm departed at 3.35 p.m. G.M.T.

the final cast the virgin queens were also shaken in a similar manner to the old queen.

A bee, when shaking the queen or another worker, usually rested its forelegs on the body, and quivered vigorously for a few seconds before departing. Occasionally the head of the worker would rest against the body of the queen and the same quivering would follow. Normally only one bee at a time would shake the queen, but sometimes more than one would take part, and the greater force resulting might then cause the queen to move. Otherwise the shaking had little apparent effect on her. It was noticed that, as Istomina-Tzvetkova stated, one worker would travel from bee to bee, shaking each in turn before passing on. In all cases observed the bee which was shaken was quite stationary before the shaking commenced, but would start moving about immediately it had finished. As far as could be ascertained no especial activity was then undertaken, and therefore it is difficult to say what was the purpose of the shaking process, but it gave the impression of being some form of communication. It could conceivably be a means of exciting both the queen and the colony in general to greater activity in preparation for swarming. The queen was certainly pushed about and treated more roughly in the week before the swarm issued. There appeared to be no particular desire to force her in a definite direction, but the aim seemed rather to be to keep her moving. On two occasions a worker was seen to bite her legs when she was stationary.

The visits of the queen to queen cells sometimes resulted in those bees on or around the cells in question quivering in the same manner as just described but without touching either her or other bees. In some cases it was a minute or more after the queen had left before the quivering ceased.

In general, only rare attempts were made to prevent the old queen examining queen cells, either sealed or unsealed, although her visits tended to cause some excitement shortly before swarming occurred. The virgins, however, were sometimes chased away from sealed cells.

On five occasions the queen was seen to lay in queen cups, but the act seemed quite voluntary and it did not appear that the bees were in any way compelling her to do so. A similar lack of interference with the queen's activities was shown during three attacks which she made on queen cells. The bees around became rather excited but showed no other reaction.

In view of the lack of detailed information on occurrences of "balling" of the queen in colonies undisturbed by man it seems useful to describe two cases observed in the present colony, particularly as they quite probably bore some relation to the swarming impulse.

The circumstances causing bees to ball their queen have not been fully elucidated, although several theories have been put forward. Balling is normally regarded either as an attempt on the part of the worker to protect the queen, or else as an attack on her, and has been recorded at various times of the year (Ribbands, 1953). Huber (1792) stated that the introduction of a queen to an already queenright stock resulted in the temporary balling of both queens before they were allowed to fight, and he also found that in certain cases a queen introduced into a queenless stock would be balled for a long period and might eventually die. On the other hand, he saw queens emerge from this balling cluster after as long as seventeen hours, apparently unharmed. He gave a detailed account of the process, noting that the guard bees near the hive entrance were the first to lay hold of the alien queen; other bees soon followed this by crowding very closely round so that a tight cluster was formed, with all the bees keeping their heads towards the centre.

In our observation hive balling was seen during the afternoons of the two days immediately preceding the formation of the first queen cup on 28th May. On both days the hive had been under observation for several hours previously, during which time there were no abnormal events, and the queen had been laying eggs in worker cells as usual. Thus, these cases differed from others recorded in not following queen introduction or examination of the hive by the beekeeper, or any other obvious possible cause.

On the first occasion the queen had just laid an egg when she was suddenly rushed at by several bees and pushed over on to one side. Almost immediately she was covered by approximately forty bees, and was not seen for about a minute, when a brief glimpse of her gave the impression that she was being cleaned. The cluster around her then was so tight that the bees in the centre were unable to move, except for their antennae. Ten minutes after the initial attack, if it was such, the queen moved out from the side of the cluster with a group of excited bees around her. The original tight cluster remained in the same place. As soon as the queen escaped she dropped three eggs in quick succession on to the surface of the comb. For a further twenty minutes the cluster remained relatively unchanged, apart from a decrease in diameter from the initial two inches to approximately one inch. Throughout there was a shell of excited bees trying to push farther into the centre. The queen now attracted no abnormal attention beyond being pushed to some extent by the bees.

About the same time on the next day a similar sequence of events started with a single worker climbing on to the queen, who moved rapidly as if trying to escape. The worker then clung on harder and bent its abdomen into a stinging position. Approximately 20 neighbouring bees quickly became excited and crowded into a tight mass about one inch in diameter, with other bees moving on the outside. The queen was now almost completely covered, but fourteen minutes later some of the bees in contact with her were seen to be licking her. After another five minutes the original worker was visible, and was still in a curved position but was also licking the queen. At first the bees at the centre of the cluster appeared excited and their abdomens were contracting and expanding vigorously, but later they were mostly still, except for the antennae. As before, those on the outskirts were continually trying to push nearer the centre. Forty minutes after the beginning of the process the position was unchanged, but once again the queen eventually emerged unharmed.

Thus, there seemed no observable reason for the queen being balled, unless it could be attributed to a change in the behaviour of the bees about to commence swarm preparations.

3. The Behaviour of the Queen

There seems to be no information as to whether the old queen attacks queen cells, although virgins are known to do so. Huber (1792) found that a mated queen attacked and opened three sealed cells which he introduced into the hive, but comments on the fact that despite the free access which old queens have to queen cells in a colony preparing to swarm, these cells are not all destroyed. He assumed in one case that seven queen cells were opened by the old queen just before leaving with the swarm, but apparently he did not observe the event.

Normally, the present queen displayed an interest in the queen cells but showed none of the animosity towards them mentioned by Huber. On three occasions, however, she was observed to damage unsealed cells. This was interesting in view of the belief that it is sealed or nearly sealed cells which are normally attacked by queens (Huber, 1792; Butler, 1954).

The first time she was seen to examine one of the cells was on 31st May. That day she visited the single queen cup five times while under observation. On one of these visits the cup had a bee working inside it and the queen could not, therefore, enter. She first tried to push the worker out from one side and then from the other, but this failing, she waited until it came out. She then went in head first and stayed for a few seconds before moving on. These occasional examinations of the queen cups continued unchanged until 10th June, when the third one was built. In the middle of the day she paid an apparently normal visit to cup No. 2, but rapidly began to cut it down. After continuing for 14 minutes about half the cup had been destroyed, and at this point the queen left. Immediately afterwards she visited cup No. 3 which was just over three inches away; she left it undamaged. By the following morning cup No. 2 was completely rebuilt, and in the middle of the morning the queen spent eight minutes cutting it down again, finally spending about two minutes inside the remains (Fig. 1). Three

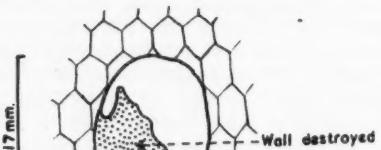

Fig. 1. Queen cup No. 6 after being damaged by queen

minutes after leaving, the queen reached cup No. 3, but departed again quickly. However, she returned again a few minutes later but was unable to look in the cell because a worker was inside, and moved away to cup No. 2 again which she did not damage further. Both cups received periodic examinations for almost another three hours and then the queen followed an examination of cup No. 3 with an attack on its walls. Three minutes later she had made an appreciable hole (Fig. 2). Leaving here she paid a visit to the now almost reconstructed cup No. 2, but quickly left and returned to destroy more of cup No. 3 for a further 16 minutes (Fig. 2).

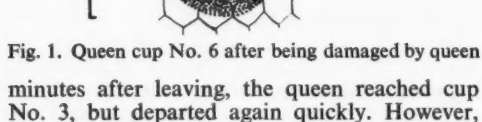

Fig. 2. Two stages of damage caused by the queen to queen cup No. 3

No more attacks on queen cells were observed that day, and by the next morning both were rebuilt. Up to 16th June the queen showed no particular interest in the queen cells, beyond examining them at intervals, but on this date she was observed to insert her abdomen into cup No. 3, which she had cut down earlier. The sequence of events was exactly similar to that when an egg was laid in a worker cell, and she was therefore assumed to be laying in the queen cup. Five minutes later she looked into two other queen cups but left without laying, only to re-examine them in fifteen minutes' time. She then looked into cup No. 3 twice and departed again, returning twice in the next forty minutes.

Rather surprisingly, considering that she had apparently chosen to lay in the queen cell and had not been forced to do so, the queen again attacked cup No. 3 during the next morning. In the nine minutes which she spent on the operation one side of the cup was damaged, but to a smaller extent than previously.

On a later date (26th June) another egg was laid in this reconstructed cup, and also in cup No. 7. The latter was again laid in three days later. The fifth and last occasion when the queen was seen to lay in a queen cup was on 5th July. During not one of these observations was she seen even to be pushed towards the cup by the bees, and it therefore seems unlikely that the process was initiated by any direct stimulus from the workers.

It is well-established that virgin queens can make the sound known as "piping" and it has been generally considered to be a challenge to unhatched queens still imprisoned in their cells. A muffled answering piping has also been heard to originate from these sealed queen cells dating from about two days before hatching. However, there appears to be no record of the old queen piping distinctly and Woods (1950) states that a relatively newly-mated queen can only produce a croaking sound. He attributes this to the reduction in volume of the air sacs caused by the pressure of the developing ovaries. Park (1949) is one of the few writers who definitely affirms that mated queens can pipe, but he gives no description of the event, nor does he explain whether he refers to young newly-mated queens or to old queens.

As is widely recognised, piping is accompanied by a regular vibration of the wings of the queen, and this made it possible to locate the source of the sound with a certainty that would have been impossible by ear alone. From this fact it can be recorded without any doubt that the year-old queen in this colony piped with gradually increasing frequency from 2nd July to 7th July, when the bees swarmed. The note produced was similar to that of the virgins heard later although there were certain slight differences which will be described below. At first the piping was heard only occasionally but by the afternoon of 4th July it occurred every few minutes. On the day of swarming it was even more frequent, occurring about once every minute.

The piping of the old queen consisted of a relatively constant number of separate notes, usually about twelve but at first nearer eight, and ultimately rising at times to about sixteen. The piping of the virgins which emerged after

the old queen had departed proved to be slightly different in form, and agreed with the description given by Park (1949). It started with one or two long notes and then became quicker, the number of notes varying greatly on different occasions. The minimum number recorded on 12th July (the day the first virgin emerged) was six and the maximum thirty-two. On this first day of adult life the virgin piped about once every fifty seconds, but by two days later she was heard more often, and the number of notes making up one group of piping had fallen to eight or nine. On this day a distinct answering piping was heard from inside the sealed queen cells. It was distinguished from that of the first virgin by being gruffer and more muffled, and also by having a longer duration (often about 30 notes). The first virgin frequently started piping again before the "answer" had been completed and this resulted in two sets of piping being heard simultaneously. During the early afternoon of 14th July the first cast left,* and by the following morning the second virgin had emerged. She piped in the same manner as the first virgin and "answering" piping was again heard, continuing until 19th July, when the last two queen cells hatched and the second and final cast issued. After this, when only one virgin and no queen cells remained in the hive, no further piping was heard.

Various authors (e.g. Langstroth, 1890) have implied that virgins pipe only when they are chased away from sealed queen cells by the bees. The present observations made it clear that piping is not confined to those times when the virgin is chased away from queen cells, but may occur, apparently quite spontaneously, on any part of the comb. On several occasions, as mentioned above, one of the virgins piped on top of a sealed queen cell but was not chased away by the bees, and on other occasions she was chased away but did not pipe. As regards the old queen, writers appear to agree that the bees do not prevent her approaching queen cells, and this had been largely confirmed here. Her piping could not, therefore, have been a result of her visits being frustrated. Nevertheless, contact with queen cells had some.connection with piping, as shown by detailed observation during a 25-minute period, commencing about an hour before the swarm left on 7th July. In this period the old queen piped 25 times. On 14 occasions she was on a queen cell, 6 times she was near one, and the remaining 5 times was elsewhere on the comb. On the previous day it was noted that she walked over queen cells on several occasions without piping, and on this and earlier days was seen piping on both sealed and unsealed worker and drone brood, as well as on queen cells.

Therefore, in spite of the fact that direct contact with queen cells does not necessarily cause either the old queen or the virgins to pipe, and although piping may occur anywhere on the comb, queen cells may be regarded as providing some special stimulus. Furthermore, piping was not heard in this colony at any time when there were no sealed queen cells present.

There has been some doubt whether the workers take any notice of the piping of the queen (Butler, 1954). Huber (1792) stated that the bees become quiet and still when the queen pipes, and this was observed in our hive. When one of the virgins piped the neighbouring bees ceased all movement (except for that of their antennae) until the sound ceased, when they resumed their normal activities.

Description of Swarming

The weather during June and July was not favourable for the departure of a swarm, being generally cold and windy, with a fair amount of cloud and some showers. There were signs that the swarm was preparing to leave on 29th June when bees were flying head-on at the entrance to the hive for about an hour in the middle of the day, but no further developments occurred. The next morning it was noticed that an abnormal number of bees were completely stationary on the bottom comb, and that at each side of the two upper combs other stationary bees were arranged with their heads upwards and their wings at an angle of 45° to their bodies, forming a column about an inch wide. By the beginning of the afternoon there was still an abnormal number of stationary bees but the arrangement was less obvious. At intervals the queen was gently pushed by the bees, which sometimes pressed their heads against her body, lifting it up slightly. Soon after, a swarm left but the queen remained in the hive in spite of being chased by the bees from the top comb to near the base of the bottom comb. It appeared as if her legs were being attacked but she was not pushed appreciably. All the swarm bees returned to the hive during the next twenty minutes, and after a further fifteen minutes a

* A cast is a swarm headed by a virgin.

normal circle of attendants had reformed round the queen.

On the following and subsequent days the same areas of quiet bees on the bottom comb and at the side of the upper combs were visible to varying degrees. It has been recognised for some time that swarm bees tend to become inactive during the period before the swarm departs but, so far as is known, this "ropey" appearance up the sides of the combs has not been described before.

The queen was sometimes pushed about the hive by the bees during these days, but, nevertheless, continued to lay, although at a reduced rate (see Table II). On 1st and 3rd July she was seen at times to be pushed away from certain of the sealed queen cells, particularly No. 4, which was the first to be sealed, but which the bees opened on 4th July to reveal a dead queen. At this time there were about 10,000 bees in the hive.

Near mid-day on 3rd July a cloud of bees was flying between the hive entrance and some small trees a few yards away, and excitement inside the hive was increasing, but two hours later the bees were calmer again. The same sequence of events occurred on 6th July and, as before, the queen kept moving throughout, while tending to avoid the lowest comb.

The weather on 7th July was similar to that of the previous day, with a dull cold morning followed by sun and some cloud in the afternoon. In the morning the bees were rather more restless than before and were fanning inside the hive. In the middle of the day for about an hour and a half there were between 100 and 200 bees (mainly on the bottom comb) head-first in the cells. It was presumed that they were emptying these cells which were known to contain honey. This phenomenon had not been seen on any of the preceding days. Soon afterwards bees were flying at the entrance in fair numbers and about this time there was the first sunshine of the day. All through the afternoon there was a double line of bees fanning in the entrance channel of the hive.

At 3.15 p.m. G.M.T. there were signs of increased excitement, with more noise and movement in the hive and more bees flying round the entrance. The queen by now was undoubtedly being pushed by one or two bees at a time. She appeared to be trying to resist and was seen to stagger on several occasions. As the excitement gradually mounted the queen was forced round and round the top and, to a lesser extent, the middle comb.

By 3.30 p.m. all the bees on the top comb were in such a state of frantic activity that they gave the impression of a seething mass streaming over the comb. The excitement was now spreading rapidly to all parts of the hive. The queen by this time had retreated to a top corner of the hive, but at this point was unable to resist any further because of the number of bees behind her, and was tumbled down the side bars of the frames to the bottom comb, where she became hidden.

The swarm issued at 3.35 p.m. and began to settle on a nearby post after some minutes. Very slowly the bees collected into a rather more compact mass, leaving considerable numbers running around the hive entrance or flying between it and the swarm.

During this time the state of affairs inside the hive was little changed except for the reduction in population. Those left were still feverishly moving about, and the queen, when she was located a few minutes after first disappearing from the observer's view, was still trying to move upwards away from the bees which were obviously attempting to force her down. The smaller numbers of bees now engaged on this operation seemed insufficient, however, and there seemed little likelihood that the queen would be made to leave the hive. For reasons which are immaterial to the present description, the queen was removed from the hive at 3.47 p.m. and shut in a small perforated zinc cage, which was then placed on top of the post over which the swarm had landed. The cage was almost immediately covered by bees, and those on the lower part of the post started moving upwards. About 10 minutes later the swarm was much more organised near the top of the post, with only a few bees remaining on the lower part, and a smaller number flying. By 4.10 p.m. all excitement at the hive entrance had ceased, although the bees left inside were restless and noisy, only quietening gradually. On the next day also the bees were abnormally excited.

It was estimated that there were 5,500 bees in the swarm.

The first virgin hatched on the morning of 12th July and, as earlier described, piped very frequently from then onwards. To distinguish her from any subsequent virgins she was marked with a small spot of white paint on the thorax.

On the 14th July she was moving more rapidly and the bees were more restless, many

flying at the entrance during the morning. At 12.35 p.m. they began running quickly up the sides of the combs, particularly the top one, and the excitement spread over all parts of the combs in a few minutes. The drones were congregated mainly on the bottom combs and a few started leaving the hive at this point (12.47 p.m.). The behaviour of the virgin was substantially similar to that of the old queen, since she was making vigorous attempts to avoid being forced out of the hive by the bees. In addition. she uttered a high pitched squealing sound at intervals.

At 12.53 p.m. the excitement had reached a great intensity and heavy rain which started to fall at 12.54 p.m. did not prevent the cast leaving two minutes later. The queen was once again not with it, but was seen in the entrance channel at 12.59 p.m. trying to force her way back into the hive. After this she was not seen for some minutes, but it was assumed from isolated squealing sounds which were heard that she was still in the hive. At 1.12 p.m. it was noted that the squealing had stopped and a few seconds later it was reported that she had been seen, surrounded by a few bees only, on the bush where part of the cast had landed.

The total size of the cast was estimated to be 1,700 bees.

By 1.40 p.m. the hive was quiet and very few bees were flying. Apart from an occasional burst of excitement round one of the sealed queen cells, and some infrequent piping, there were no abnormal events for the rest of the day.

The second virgin emerged during the following morning and piped loudly from then onwards. She was marked distinctively with white paint soon after emergence. The behaviour of the bees followed the customary pattern of the last few days, with an abnormal amount of excitement and bees flying near the entrance, but swarming pitch was not reached until 19th July. At 12.15 p.m. G.M.T. greater excitement started than on the two previous occasions and a very large number of bees forced the virgin down. She fought the bees continually and succeeded in approaching closely to queen cells Nos. 6 and 8 about twenty times, but was always pushed away by the moving bees.

At 12.30 and 12.35 p.m. respectively these two queen cells hatched, but although there were then three virgins free in the hive they were not seen to come into contact with one another. Immediately on hatching, the virgin from cell No. 8 walked about three inches away and was then seized by about twelve bees which clustered round her and pinned her on the comb. The group remained immobile for about two minutes and then the virgin gradually fought clear and was not attacked any more.

At 12.40 p.m. it was noted that the other two virgins could not be seen and at this time the cast actually left the hive.

The cast landed in two distinct sections less than a foot apart, one on a branch and the other on the trunk of a tree. Further examination showed that the second virgin (distinguished by the white mark) was in the first section, and one of the newly-emerged virgins in the second.

All was quiet inside the hive at 1.00 p.m., and by 3.00 p.m. every queen cell had been cut down. The colony thus resumed normal life at a strength of rather less than 1,500 bees (which cover about half a British Standard brood comb). The swarming impulse therefore continued until the colony had lost so many bees that it was far too small to survive the following winter.

The disinclination of the queens to depart with the swarm has been observed by other workers (including Taranov & Ivanova, 1946). Langstroth (1890) states that the queen often leaves the hive only after much of the swarm has departed and may sometimes not join the swarm until the cluster has begun to form, thus possibly indicating some reluctance to go with it.

The excitement which develops in a colony on the point of swarming has to some extent been reported before, but even Huber (1792) does not convey the tremendous pitch to which it rises in the few minutes before the swarm starts to leave. He was under the impression that the queen caused the excitement among the bees by becoming rather agitated herself and moving all over the combs. The bees became excited by her passage and transmitted their excitement to others, until the whole colony was in the same state He believed that the departure of subsequent casts was similarly precipitated by the virgins rushing about the hive, but in this case the excitement of the virgins was in his opinion, a direct result of their being continually chased away from the sealed queen cells by the workers.

As far as the present colony was concerned, the passage of the old queen through the hive did appear to increase the excitement of the bees in her path, but her movements were

almost certainly not voluntary, but were a result of some of the bees forcing her through the already excited colony. Thus, while the presence of a queen is absolutely essential in a swarm, she presumably plays little part in deciding when it shall depart and, furthermore, is likely to attempt to remain behind when it goes.

Summary

1. A 3-frame observation hive was used to study the events leading up to swarming in a colony of bees with a year-old queen.

2. The first queen cup was built on 28th May and a further seventeen were built between 9th June and 14th July. Four virgins hatched from these cells.

3. A prime swarm and two casts reduced the strength of the colony from approximately 10,000 bees just before swarming to approximately 1,500 bees finally.

4. The queen continued to lay until the day of swarming, and on five occasions was seen to lay in queen cups without any apparent compulsion from the workers.

5. The queen was only once or twice prevented from carrying out frequent examinations of the queen cups.

6. She was not interfered with on three occasions when she tore down unsealed queen cells, although the bees became rather excited at these times.

7. There was a reduction in the number of attendants feeding the queen after queen cell formation had begun, the bees often refusing to supply her with food, and the mean age of bees feeding the queen decreased as the swarming urge developed.

8. Two cases of "balling" of the queen are described.

9. Certain workers were seen sometimes to "shake" the queen or other workers, and this process is described. It increased in frequency as the swarming preparations developed.

10. A year-old mated queen can "pipe." Commencing five days before the swarm left, this piping became very frequent in the final two days. Unhatched virgins piped, and after hatching they piped much more frequently. Piping ended after the final cast had departed. Descriptions of piping are given.

11. Bees in the neighbourhood of a piping virgin became quiet and still until the piping ceased.

12. A feature of the few days preceding swarming was the appearance of columns of stationary bees at the sides of the combs.

13. Intense activity, in which all the bees took part, immediately preceded the issue of the swarms.

14. Both the old queen and the virgins vigorously resisted the efforts of the workers to push them out of the hive with the swarms.

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STUDIES OF FIGHTING IN CHAFFINCHES
(3) PROXIMITY AS A CAUSE OF AGGRESSION

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During a study of fighting among non-reproductive Chaffinches it was observed that when both wild (Marler, In Press) and captive individuals (Marler, 1955, a, b) came into close proximity with each other, a fight always developed. This occurred during competition for food, water, favourite perches, etc., and also when birds accidentally alighted close together. These experiments were designed to measure the actual distance to which one bird must approach another, before fighting occurs.

Methods

Food was used to bring the birds into proximity. The experiments were conducted in winter, with birds in non-reproductive condition. Each cage (2m. × 2m. × 2m.) containing eight birds was provided with a pair of food hoppers, at each of which only one bird could feed at a time (Plate I, Fig. 1). The distance between them could be adjusted, and the effect observed on the incidence of fighting among feeding birds. The distance between the adjacent ends of the hoppers was noted each time. At zero distance it was just physically possible for the birds to feed (Fig. 1). Between experiments the hoppers were placed far enough apart for aggression to be avoided. Each experiment, lasting thirty minutes, was conducted with a different distance, changed randomly in successive tests. Each distance was tested again after an interval of several days.

Each time both hoppers became occupied an "encounter" was recorded. These were divided simply into two groups. Those in which both birds held their positions, with or without aggressive or submissive display (see Marler, In Press) were classed as "non-aggressions," those in which one bird drove another away, as "aggressions." This clear division was used to avoid the difficult alternative of deciding when aggressive display was present or absent.

The results are presented as a ratio of non-aggressions: total encounters ($^n/t$). Thus the closer the ratio approaches 1.0, the larger is the proportion of non-aggressions.

Experiments with Females

In two flocks of 8 females, 669 and 931 encounters were observed. The number increased with the distance between the perches. This is to be expected since the flocks were organised in peck-right hierarchies (Marler, 1955 a), and both here and under normal conditions, subordinates tended to avoid proximity with dominant individuals. Figure 2 shows the results of encounters, expressed as a ratio of non-aggressions: total encounters, plotted graphically against the distance between perches.

Non-aggressions clearly became less frequent as the distance between hoppers decreased, and ceased when the perches were touching. The results are most easily summarised by extrapolating on each curve that distance at which non-aggressions make up half of the encounters ($^n/t=0.5$). This "50 per cent." distance is about 7 cm. in both flocks. Thus, when two females alight this distance apart, there is an even chance that a fight will occur. From the shape of the curves it is evident that there is no sharp threshold beyond which aggression occurs, but rather a gradient, along which the probability of aggression gradually increases. Some birds might allow subordinates to come closer than others. These variations, averaged out in the curve, would have the effect of decreasing its slope and making the threshold appear more gradual than is actually the case. The results were therefore rearranged to show the behaviour of particular birds. Figure 3 shows the results for the three top ranking individuals (1-3) towards all their subordinates. The variation is considerable, and while in one case (3) the threshold is abrupt, in the other two the slope is more gradual than that for the whole flock. Thus birds do not necessarily have a clear threshold distance for all subordinates, though this may occur in some cases. Again it might be that the same bird treats individual subordinates differently. The results were therefore rearranged to show the outcome of encounters between particular pairs of birds.

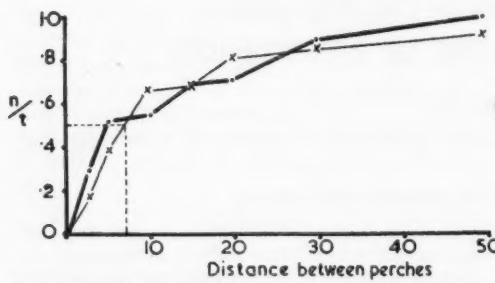


Fig. 2. A graph of the ratio of the number of occasions when two birds fed without fighting, to the total number of encounters (non-aggressions/total = n/t) plotted against distance between the perches, in two flocks of eight females. The 50 per cent. distance, extra-polated for a value of n/t = 0.5, is 7 cm. in each case.

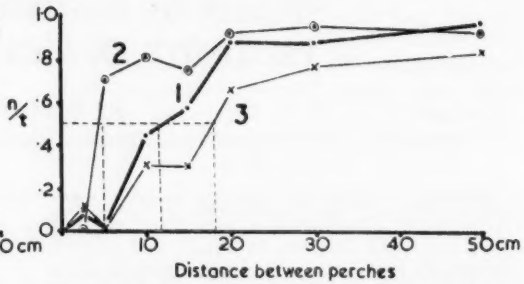


Fig. 3. Results for three females, towards all their subordinates. The numbers 1-3 indicate positions in the hierarchy. The 50 per cent. distances are 5 cm., 12 cm. and 18 cm.

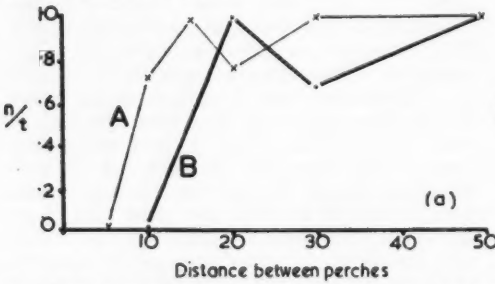
In most cases the numbers of observations were not sufficient to be reliable, but contacts between two birds (2 and 3 in Figure 3) and two of their subordinates are shown in Figure 4. Clearly the same bird may have different thresholds towards different subordinates. Also the gradients appear steeper than in the summarised results of the flock.

It will be noted that the bird showing the clearest threshold towards all subordinates (bird 2 in Figure 3) shows least differences in behaviour towards the two subordinates (Fig. 4a). The reverse is true of bird 3 (Figs. 3 and 4b). Thus the gradient of the curve may be to some extent related to the degree of sensitivity to the individuality (or behaviour, see page 27) of subordinates. It is interesting to note that the top ranking bird (bird 1, Fig. 3) does not have the highest 50 per cent. distance, though this must provide some measure of aggressiveness. However, it is known in other species that many things besides aggressiveness can contribute to status in the hierarchy (Ginsburg & Allee, 1942; Collias, 1944).

Experiments with Males

Male Chaffinches dominate females in the social hierarchy (Marler, 1955 a) and appear more aggressive. To determine whether this is manifest in their sensitivity to proximity, two flocks of eight males were studied. The numbers of encounters increased with distance between hoppers, from 35 at zero distance to 124 at 50 cm. in flock 1, and from 35 at zero distance to 183 at 65 cm. in flock 2. Fig. 5 shows the results of these encounters. As in the female flocks, non-aggressions became less frequent as hoppers were closer, and virtually ceased at 10 cm. The 50 per cent. distance was 21 cm. in flock 1 and 24 cm. in flock 2.

Thus the distance at which males are as likely as not to fight is about three times greater than the corresponding distance for females. The more gradual gradients, however, show that they are more variable in their behaviour than females. It will be noted that neither of the curves reaches the asymptote even at a distance of 50 cm. This is probably because many males while feeding under these aviary conditions,



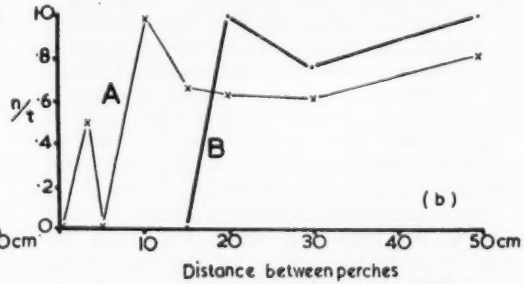


Fig. 4a and b. Results for two females, bird 2(a) and 3(b) in the hierarchy against individual subordinates, two in each case

PLATE I

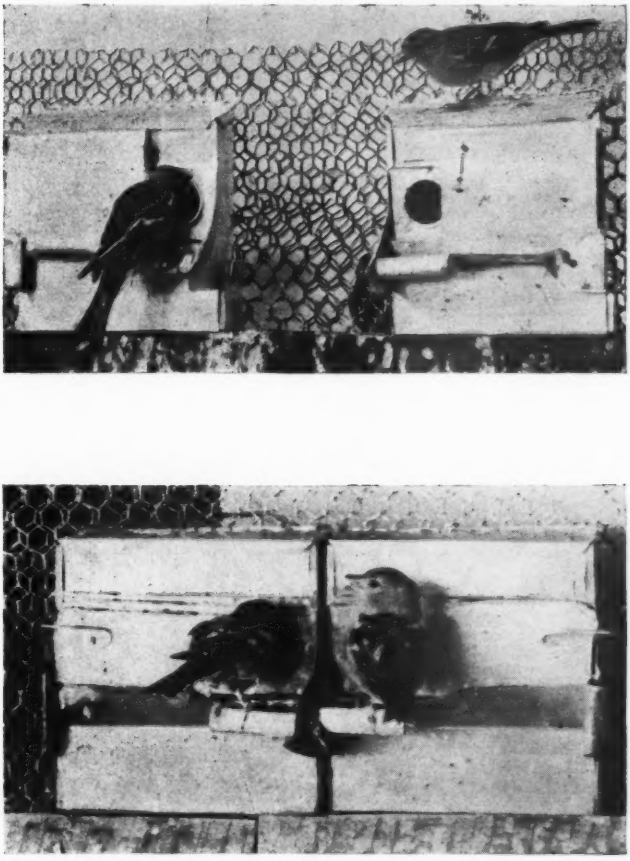


Plate I. Fig. 1. The arrangement of food hoppers for testing the distance at which feeding birds would tolerate each other. Above : one male about to attack another, at 10 cm. Below : two females feeding at zero distance.

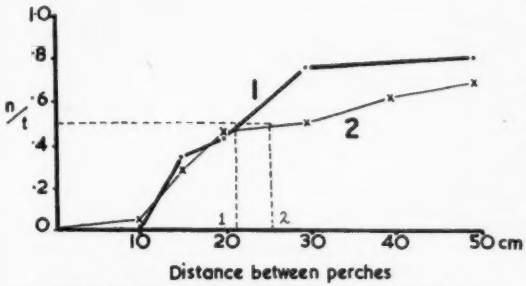


Fig. 5. Results for two flocks of eight males (see Fig. 2). The 50 per cent. distances are 21 cm. and 25 cm.

moved restlessly from hopper to hopper, however far apart they were. This brought them into proximity with other birds, and thus caused more fights than would otherwise occur. Females were less restless and the curve approaches the asymptote more closely (Fig. 2).

Experiments with Males and Females

It was found in other experiments (Marler, 1955 a) that males were more tolerant of females than of other males. To investigate this further, two flocks were studied, each of 4 males and 4 females. Fig. 6 shows the results, divided into male-female, male-male and female-female encounters. The 50 per cent. distances of the two latter agree approximately with those found in the previous experiments, 21 cm. and 18 cm. for male-male encounters, 10 cm. and 12 cm. for female-female encounters. In male-female encounters the 50 per cent. distance was found to be 12 cm. in flock 1 and 8 cm. in flock 2 — about half of the corresponding male-male distances. In fact, a female can approach as close or closer to a male than to another female before fighting develops.

Experiments with Red-dyed Females

In a previous series of experiments it was found that the male redbreast is an important stimulus in sex recognition. Using a similar technique, females with red-dyed breast feathers were tested with the distance hoppers. Two flocks of 4 males were each matched first against 4 normal females, then against 4 "red" females, and finally against another 4 normal females. The results are divided into male-normal female (1st and 2nd series) and male-"red" female encounters (Fig. 7).

The same males were used in the previous experiments and the 50 per cent. distances for male-male encounters were found to be 21 cm. in flock 1 and 18 cm. in flock 2. In the present experiment the 50 per cent. distances in male-"red" female encounters were 23 cm. in flock 1 and 16 cm. in flock 2, and in the control experiments with normal females, 12 cm. and 6 cm. in flock 1, 8 cm. and 9 cm. in flock 2. Thus while a male would allow a normal female to approach to within about 10 cm. of him before attacking, a red-breasted female was attacked at about 20 cm. In fact a "red" female was treated as though it were a male.

The red breast is also significant to females in fighting and it is of interest to know at what distances "red" females will tolerate each other. This can be derived from the above experiment, though the figures are small and somewhat irregular. Figure 8 shows the "red" female-"red" female and the two normal female-normal female curves for each flock. In spite of the irregularity it is clear that "red" females respond to each other as though they were males, with 50 per cent. distances estimated at 25 cm. in each case.

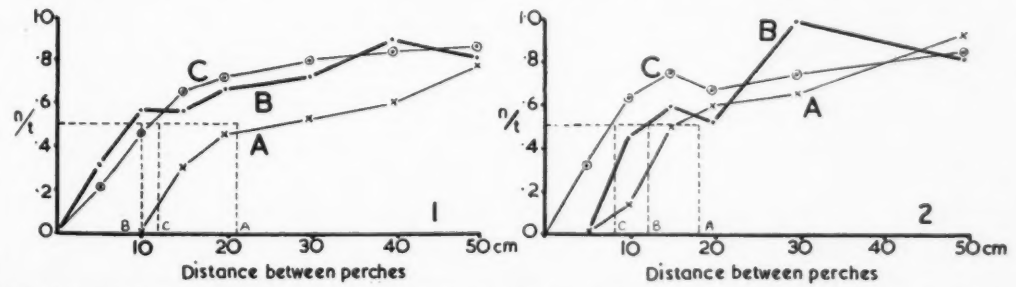


Fig. 6. Results for two mixed flocks, each of four males and four females (see Fig. 2). They are divided into male-male (A), female-female (B), and male-female encounters (C). The 50 per cent. distances are A—21 cm. and 18 cm., B—10 cm. and 12 cm., C—12 cm. and 8 cm.

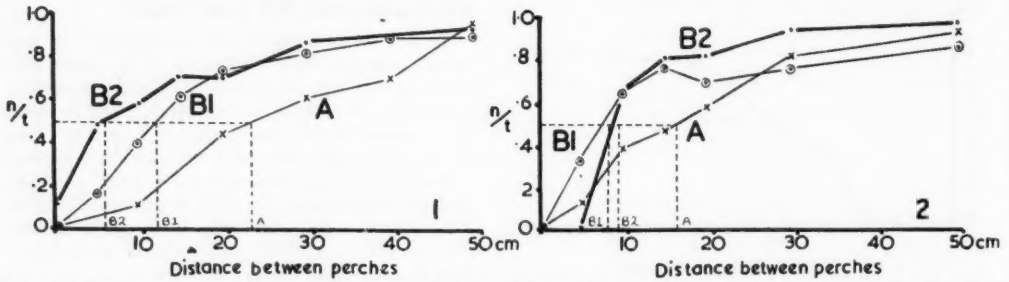


Fig. 7. Results for two experiments in each of which four males were tested with four normal females (B1), four females disguised as males (A), and then with four more normal females (B2), (see Fig. 2). The 50 per cent. distances are A—21 cm. and 18 cm., B1—12 cm. and 8 cm., B2—6 cm. and 9 cm.

In general, males dominated both "red" and normal females in the above experiments, but as in previous experiments some "red" females dominated males. Because of the small figures (269 encounters in flock 1, 36 in flock 2) the curves for encounters between these "red" females and subordinate males are very irregular (Fig. 9). But in both flocks they suggested 50 per cent. distances between 20-30 cm., of the same order as in "red" female-"red" female encounters.

To study the relationship between "red" females and normal females, a further series of experiments were conducted with 4 "red" and 7 normal females. As in previous experiments most "red" females dominated the normal ones. In encounters between "red" females and their normal subordinates (Fig. 10) a very small 50 per cent. distance was recorded —3 cm. Thus "red" females responded as both females and males do to normal subordinate females, by allowing them to come very close before attacking them. Conversely normal females approached close to dominant "red" females, as they would to males.

Thirty-one encounters were recorded between normal females and subordinate "red" females. The results suggested, very approximately, a 50 per cent. distance of about 15 cm., considerably greater than that for encounters between normal females.

It may be concluded from these experiments with red-dyed females that a Chaffinch of either sex will allow subordinates with a red breast to approach to within about 20 cm. before it is likely to attack them. Those lacking the red breast may approach to within less than half this distance.

This leads to a conclusion of the greatest interest, that using the distance at which others are attacked as a measure of aggressiveness, females are potentially no less aggressive than males. The apparently greater aggressiveness among males only occurs because they all carry male colours. Females disguised as males behave similarly. The fact that such females sometimes dominate males in the social hierarchy (Marler, 1955 b) suggests a similar conclusion. In both cases, the behaviour of disguised females is to be explained, not by a direct effect of colouring on

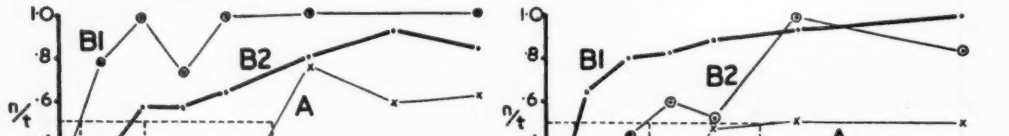


Fig. 8. Results for normal female-normal female (B1 and 2) and "red" female-"red" female encounters (A), in two series of experiments (see Fig. 2). Each curve represents the results for four different birds.

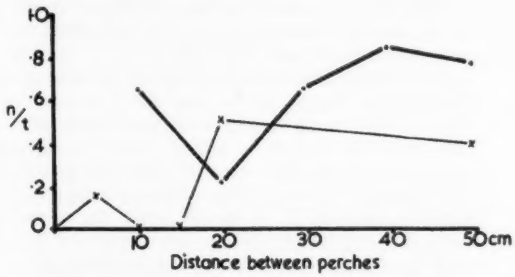


Fig. 9. Results for "red" female-subordinate male encounters in two flocks (see Fig. 2).

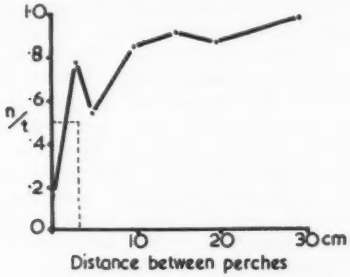


Fig. 10. Results for "red" female-subordinate, normal female encounters, in a flock consisting of four "red" and seven normal females (see Fig. 2).

their own aggressiveness, but by their responsiveness to the changed behaviour of others towards them.

The Effects of Starvation

In connection with other experiments (Marler, 1955 a) it was of interest to observe whether starvation affected aggressiveness, as revealed by how close other birds were tolerated. A flock of 8 males was watched for 30 minute periods, after 45, 90 and 180 minutes of starvation, with the food hoppers set 20 cm. apart. Each was preceded on the same day by a control period of observation without starvation, and was repeated twice with never more than one experiment per day.

Table I shows the ratios of non-aggressions: total encounters ($^n/_t$) in all starvation experiments. Clearly none of them differ significantly from their controls. Starvation periods of this order were known to have marked effects on fighting behaviour. The numbers of control encounters: experimental encounters were 229: 335 after 45 minutes, 162 : 341 after 90 minutes and 120 : 356 after 180 minutes of starvation. Thus there was a considerable increase in the number of encounters at the food, but nevertheless no effect on the distance at which other males were tolerated was revealed.

There was an interesting tendency for the proportion of non-aggressions to increase in experiments and controls alike during the period of a month in which they were conducted (Table I, in the order 45m. 90m 120m.) The decrease in the number of control encounters may be related to this, since with less aggression, birds made fewer visits of longer duation to the food (cf. Marler, 1955 a).

The explanation of this is not known, but it may result from a form of habituation (Thorpe, 1950). Under crowded conditions, with competition for food imposed, it may be that fighting becomes unrewarding. A bird loses valuable feeding time by repeatedly breaking off to attack others. In these circumstances birds may sometimes learn to concentrate on feeding rather than fighting.

The Effect of Behaviour

It has been emphasised that there is no sudden threshold beyond which another bird is always attacked but rather a gradient, more or less

Table I. The Ratio of n/t (see Fig. 2) in a Flock of Eight Males With the Food Hoppers set 20 cm. Apart, after various Starvation Periods. Each starvation experiment was preceded by control observations without starvation, and was repeated in three experiments.

	EXPT. 1.		EXPT. 2.		EXPT. 3.		TOTAL RESULTS	
	Unstarved Controls	Starved	Unstarved Controls	Starved	Unstarved Controls	Starved	Unstarved Controls	Starved
45 minutes starvation	.64	.62	.59	.63	.64	.62	.62	.62
90 minutes starvation	.62	.63	.69	.64	.65	.70	.65	.65
180 minutes starvation	.66	.65	.66	.75	.69	.70	.67	.70

steep in different individuals, along which the probability of attack increases. One of the factors making for variability, revealed by qualitative observation, is the effect of the behaviour of the opponent. In general birds showing submissive behaviour can come closest, then those showing normal alert behaviour, those in escape postures, and finally those showing aggressive behaviour are attacked furthest away. Also there is a suggestion that birds may come closer in the horizontal than in the vertical plane.

"Contact" and "Distance" Animals, and the Concept of "Individual Distance"

Hediger (1942) has suggested that animals can be roughly divided into two groups, those which seek bodily contact with each other—contact animals—and those which normally avoid bodily contact—distance animals. These categories may appear to be artificially clear in captive animals. They are best defined by whether the animal will tolerate contact, or not. "Contact" animals are not, of course, always touching. Their dispersal may result merely from random spreading without a positive avoidance of contact, or may be a form of over-dispersal, in which case a change must be postulated from "contact" to "distance" behaviour. Both are found among birds. The contact type is found among some very small species, e.g. the Long-tailed Titmouse, *Aegithalos caudatus*, (Hinde, 1952), and some Ploceid finches, which perhaps huddle together to keep each other warm. This certainly explains the contact behaviour of the Emperor Penguin, *Aptenodytes forsteri* (Stonehouse, 1953). The distance type is much more widespread. To the already considerable list (see Hediger, 1942; Burckhardt, 1944; Conder, 1949; Hinde, 1952) we may add the Chaffinch, and also the Bullfinch, *Pyrrhula pyrrhula*, the Hawfinch, *Coccothraustes coccothraustes*, the Goldfinch, *Carduelis carduelis* and the Greenfinch, *Chloris chloris*. Except when copulating, or feeding the mate or the young, these species always avoid bodily contact.

Hediger (1942) advanced the idea of individual distance, since applied and developed by Burckhardt (1944), Conder (1949) and Hinde (1952), as an area around the individual which is kept free of all others, either by attacking intruders, or by moving away from them. This clearly corresponds with the phenomenon that has been studied here in the Chaffinch.

Individual distance in the Chaffinch is seen to be readily measurable, and to vary with the sex, behaviour and individuality of the intruder. In general it does not seem to vary with the internal state, in winter. Thus a starved male is no more or less tolerant than when satiated. An exception occurs when two birds alight close together on the same perch while fleeing from a hawk. They will stay within each other's individual distance until the escape response has waned, when one attacks or flees, and they part. Here a strong tendency to escape directly interferes with fighting behaviour by suppressing signs of aggression. This interaction occurs in every fight, but whereas it is usually only evident in the loser, here it affects both combatants, and fighting is therefore temporarily suspended.

Variation in individual distance may occur in other species. Conder (1949) suggests that it is less when Black-headed Gulls, *Larus ridibundus*, are resting than when they are searching for food. He also points out that it may disappear temporarily among Tufted Ducks when they are scrambling for food. Crook (1953) describes in more detail the variation in Black-headed Gulls during different feeding activities. Something similar may occur during communal roosting in certain species, which are normally intolerant of proximity during the day (e.g. the Wren, *Troglodytes troglodytes*, Armstrong 1955). Some examples however may be explained by an interference with capacity to perceive other individuals (e.g. by darkness), by a change in the usual tendency to focus "attention" on them (e.g. during scrambling for food), or by inhibition of aggression by a strong, incompatible tendency (e.g. to roost), rather than by a real change in individual distance. And there are often signs of tension when birds are close, even though actual fighting does not develop (e.g. Crook, 1953).

Individual Distance and Territory

Many animals defend territories in the breeding season. The area which an individual defends is usually centred on some object or collection of objects, often essential for reproduction. It may occupy a fixed position in space, like the breeding territories of most song birds, or may be centred on something that moves around, such as a host, mate or young. The only obvious difference between territories of this kind, which have been much studied (e.g. Nice, 1941; Tinbergen, 1953), and individual distance,

is that the latter is centred on the individual itself rather than on some external object.

Conder (1949) has argued that the various types of defended area are also developmentally related to individual distance. He describes small, mobile territories set up by birds on migration which appear to be intermediate between individual distance and fixed territory. He gives evidence that other species have a third phase, a territory centred on the female, interposed between individual distance and the development of the breeding territory. Male Chaffinches in early spring also show an enlarged individual distance that moves with the bird, probably only appearing in the area that will become the territory, (Marler, in press). This is followed by an intensification of aggressiveness at certain points which expand into the whole breeding territory.

Even the most conspicuous characteristic of territorial behaviour, namely the effect of immediate surroundings on aggressiveness, is not without parallel in individual distance behaviour. An intruder within the individual distance may be attacked or avoided. One of the factors determining the course that is taken is familiarity with the surroundings, which encourages attack. Thus Chaffinches familiar with the cage in winter usually dominate newcomers (Hinde, 1953), and wild Juncos, *Juncos hyemalis*, and Tree Sparrows, *Spizella arborea*, that are strangers to the winter feeding area, are dominated by the local residents (Sabine, 1949).

Thus there are good reasons to believe that individual distance is directly related to the defence of other types of area. One may go further and suggest that it is the simplest and most primitive form of defended area, and is perhaps the evolutionary precursor of the other types that have been described.

It is generally agreed that while the defended area may discourage epidemics, or restrict certain kinds of predation of cryptic animals (Tinbergen, 1953), it usually also provides something essential for life or reproduction, for which the defender is competing with other individuals. It is important to emphasise the importance of competition, for it would surely be dysgenic to fight for something not in fact in limited supply. Limitation of the supply of some essential commodity will always tend to encourage the aggregation of individuals around the remaining sources, which in turn will bring individuals into proximity. One can readily imagine the tendency developing, in such circumstances, to defend an area around the individual, as the most economical method of defending the individual's needs. By placing himself close to the object competed for, and attacking all who come too close to him, he would increase his chances of retaining it.

This relatively simple mechanism would help to obtain anything required, such as food, water, mate, nest, or space, and would avoid unnecessary fighting, since intrusion of individual distance would be rare in conditions of abundance. Once established, it is easy to imagine it expanding or contracting according to the particular requirement of the species. Thus a dispersed food supply would call for a larger individual distance than a concentrated one. Other requirements would be better satisfied by fixing the defended area in space—e.g. the need for mates to keep in contact for the whole of the breeding season, or to tend eggs or young. Various specialised territories would develop, culminating in the breeding territory, which is as varied and versatile in function in summer, as individual distance is in winter. And since all types result in some degree of over-dispersal, they may from their very inception have served several functions at once of the many that have been proposed in the past.

Summary

1. It was found that whenever two Chaffinches (*Fringilla coelebs*), in winter, alighted close together, a fight resulted. Experiments were conducted, using movable feeding hoppers to bring birds close together, to measure the distance at which one individual attacked another.

2. The results reveal a zone, rather than an abrupt threshold distance around each individual, across which the probability of aggression increases. A convenient measure is provided by the "50 per cent. distance," at which there is an even chance of two birds fighting or tolerating each other. This distance was 7 cm. in two flocks of eight females, 21 cm. and 25 cm. in two flocks of eight males.

3. Individual females would allow some subordinates to come closer than others. The bird at the top of the social hierarchy was not necessarily the least tolerant.

4. In flocks of both sexes (in which males normally dominated females) males allowed females to come much closer than other males, before attacking them. Females disguised as

males, by dyeing the breast feathers red, however, were treated as though they were males.

5. The disguised females also responded to each other as though they were males, by attacking at greater distances than normal females would.

6. It is concluded that the apparently greater aggressiveness of males in winter results from their responses to each other's colouration, especially the red breast.

7. Moderate starvation had no effect on the distance at which males attacked each other.

8. Behaviour affected the distance at which others are tolerated, birds showing submissive behaviour being allowed to come closest, while those showing aggressive behaviour were attacked at the greatest distance.

9. The findings are related to the idea of individual distance, a defended area around the individual, which is directly related to various forms of territorial behaviour, and is perhaps the most primitive type.

Acknowledgments

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CONDITIONED RESPONSES IN RATS REINFORCED BY LIGHT

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It has been generally held that rats, being primarily nocturnal animals, are light shy. A number of investigators have used strong light as an adversive stimulus to set up and sustain avoidant conditioned responses. However, recent research completed in our laboratory shows that weak light may serve as an incentive and lead to the formation of strong adient conditioned responses. Both Girdner (1953) and Henderson (1953) have made similar observations in recently reported, independently conducted, investigations.

In our experiments twelve male hooded rats, 2½ months old, drawn from the inbred colony maintained by the Department, were placed on a rigorous feeding schedule. Unlimited food was made available once daily between 6 and 8 p.m. During feeding time, the laboratory was darkened, so as to minimise the association of food and light. This regime was started six weeks before the beginning of the experiments and was maintained throughout the experimental period. The animals were allocated at random to three groups, each of four animals. Each group underwent a different series of tests in a very simple apparatus, consisting of a rectangular box (of base 8½″ × 12½″ and 12½″ high), placed into a sound-proofed dark chamber. A lever (½″ × ½″) responding to 3 g. pressure was mounted 3″ above floor level in one corner. A 6-volt light bulb was mounted on a wall at the opposite end of the box, 10″ above floor level.

Three experimental conditions were set up.

Box totally dark except that when the lever was pressed a light (5.2 candle power) was switched on for as long as the lever was held down; alternatively, the lever switched a light off.

Box illuminated by a 5.2 c.p. lamp except that for the period the lever was held down, the light was extinguished.

Box in total darkness at all times.

Each animal subjected successively and for a varying number of trials to the experimental conditions indicated in Table 1.

After six weeks of the feeding schedule each animal was placed into the box for a half-hour daily session before feeding time. At the conclusion of each trial, the animal was placed in a darkened feeding cage, to exclude any association between light and food. This procedure should favour the association of darkness and food. Records were obtained of the total *number* of lever pressing responses on each trial, the *duration* of each lever pressing response and the *rate* of lever pressing response in

Table I. Survey of the Design of the Study

Group	Successive order of experimental conditions	No. of ½-hour trials	Experimental Conditions
A (4 animals)	A I	10	Lever pressing in dark box has no after effect
	A II	12	Lever turns a light on
	A III	10	Lever turns light off
B (4 animals)	B I	5	Lever turns a light off
	B II	10	Lever turns a light on
C (4 animals)	C I	16	Lever turns a light on
	C II	6	Lever pressing in dark box has no after effect
	C III	10	Lever turns a light on

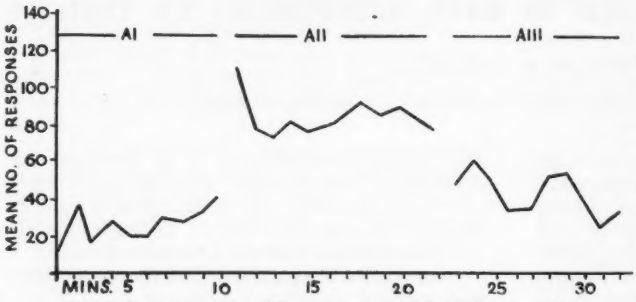

Fig. 1. Mean number of Responses per daily half-hour trial.
AI: lever——>no after effect; AII: lever——>light on;
AIII: lever——>—light off.

successive trials. The present report deals mainly with the first of these measures, which are summarised in Figures 1-3.

Two features of the results should be noted.

Experiment A-I shows that when the lever pressing is unattended by any perceptible after-effect in a dark box, the frequency of response stabilises in the present instance at about 30 responses per half hour. When, subsequently, the response is instrumental in switching on the light the response frequency immediately increases and after an initial high value stabilises at about 85 responses per half hour. The scores under condition A-II and A-III or A-II and B-I show that the higher response frequency observed under conditions A-II, B-II, C-I and C-III is correlated with the *onset* of light: when the animal's actions turn off the light, as in experiments A-III and B-I, the response frequency does not differ significantly from conditions A-I. An interpretation of similar results proposed separately by Girdner (1953) and Marx, *et al.* (1955) that the animals' performance and learning is due to curiosity or novelty, cannot readily be reconciled with these observations. Such an interpretation predicts no difference in the frequencies of response between conditions of switching on or switching off the light.

The results of experiments A-II and C-I contrast sharply, despite identical conditions of observation. Throughout the 16 trials of experiment C-I, the frequency of response per trial increased and again increased in experiment C-III, whereas the response occurred most frequently on the very first trial of experiment A-II. A tentative explanation of this difference will be attempted elsewhere. For the present, our main interest lies in the steady increase of the frequency score throughout successive trials in experiment C-I, the decline in response frequency during experiment C-II and the recovery of high response frequency in the final experiment C-III. These results are comparable to conditioning, experimental extinction and reconditioning phenomena described by Skinner (1938) and previously by Pavlov (1927) in his classic studies of conditional reflex learning, and are being interpreted in this manner by the writer. The increasing frequency of response during successive trials in C-I is regarded as indicative of the systematic strengthening of a conditioned response based on the incentive (and reinforcing) function of light. When the incentive is dissociated from the response, as in experiment C-II, a gradual waning of the response (shown by a decrease in frequency) is predicted, the rate of response deterioration

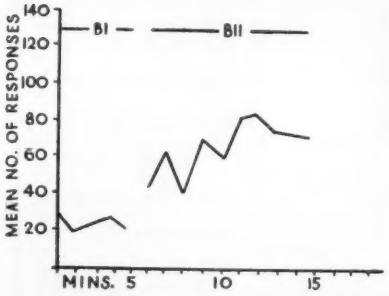

Fig. 2. Mean number of Responses per daily half-hour trials.
BI: lever——>light off; BII: lever——>light on

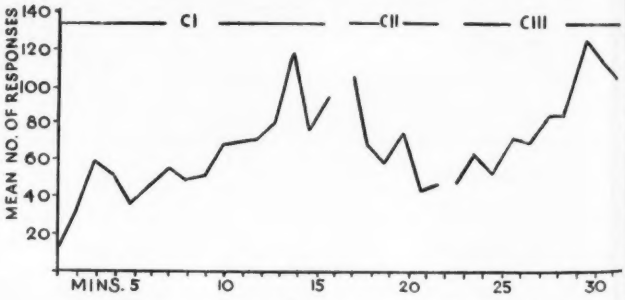

Fig. 3. Mean number of Responses per daily half-hour trial.
CI: lever——>light on; CII: lever——>no after effect;
CIII: lever——>light on

being a joint function of the incentive value of the reinforcing stimulus and the strength of the conditioned response.

These interpretations are supported by the data of *duration* on the lever holding response. When light accompanies the lever-response, the average duration of the response is significantly longer than under conditions A-I. We have recorded durations extending up to 5 minutes, although the mean value in experiment C-I is 2.3 seconds are compared to .3 seconds in A-I.

When the light is kept on for extended periods, the animal vigorously surveys the box, making rapid, scanning-like head movements. The rate of pressing was not regular. Responses tended to be bunched, each 'burst' being separated by periods of 'silence.' During a response burst the animal would stand on its hind legs in front of the lever, resting one or both on its paws on the lever, the head held at right angles pointing to the light source. An infra-red film is being made to discover the animal's behaviour during "silent" periods. The analysis of the animal's total activity during the response-bursts and silent periods should help to clarify the obviously puzzling problem inherent in the experimental results so far cited.

The above results are relevant to the controversy about the importance of homeostatic mechanisms in animal learning which continues to feature prominently in the literature on the psychology of learning. Some writers (Hull, 1943) hold that the conditioning of responses is only possible in the presence of stimuli representative of need stabilisation. So far, at least, it has been extraordinarily difficult to adduce evidence inimical to this theory. However, since it is not obvious how light—in the case of rats—is instrumental to the stabilisation of organic needs, it seems that the experiments reported here, as well as those reported by Girdner (1953), Henderson (1953) and Marx *et al.* (1955) call for an alternative approach to the central problems of conditioning.

Acknowledgment

This study has been supported by a grant from the Central Research Fund, University of London.

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OBSERVATIONS ON THE SUCKLING BEHAVIOUR OF YOUNG LAMBS

By JOAN MUNRO

Department of Agriculture, University of Aberdeen

The dependence of the young lamb on the milk supply of the ewe is known, and the amounts of milk consumed by the young lamb have been estimated in experiments by weighing the lamb before and after suckling at intervals of three or four hours. In lactating sows, it has been shown that milk yield is grossly underestimated if the intervals between recordings are from two to six hours (Barber *et al* (unpublished) *cit.* Braude, 1954). Young piglets suckle at approximately 1-hour intervals, regardless of age, and reliable estimation of the sow's milk yield is made by allowing the piglets to suckle every hour.

It is possible that ewe milk yields may be affected by the length of time between sucklings and this investigation was undertaken to find the natural suckling behaviour of young lambs.

Experiment

The experiment began with 2 Blackface cast ewes, each with twin lambs. The twin lambs were 7 and 9 days old at the beginning of the investigation and they were observed once each week for 6 weeks.

Suckling behaviour in twin lambs was recorded by observing them directly during the hours of daylight. Attempts to observe the sheep during darkness failed, even when luminescent substances were smeared on the animals. Observations, therefore, ended after darkness had fallen and began again before dawn. It was not found possible for a single observer to watch continuously throughout a complete solar day but observation times were arranged to cover a complete day in not more than 3 periods of continuous observation.

The twin lambs were replaced by 2 Blackface cast ewes with single lambs. One single lamb was newly born and the other aged 3 weeks. The behaviour of the twins had shown that shorter periods of observation would give a reliable estimation of suckling times, and observations were therefore limited to periods

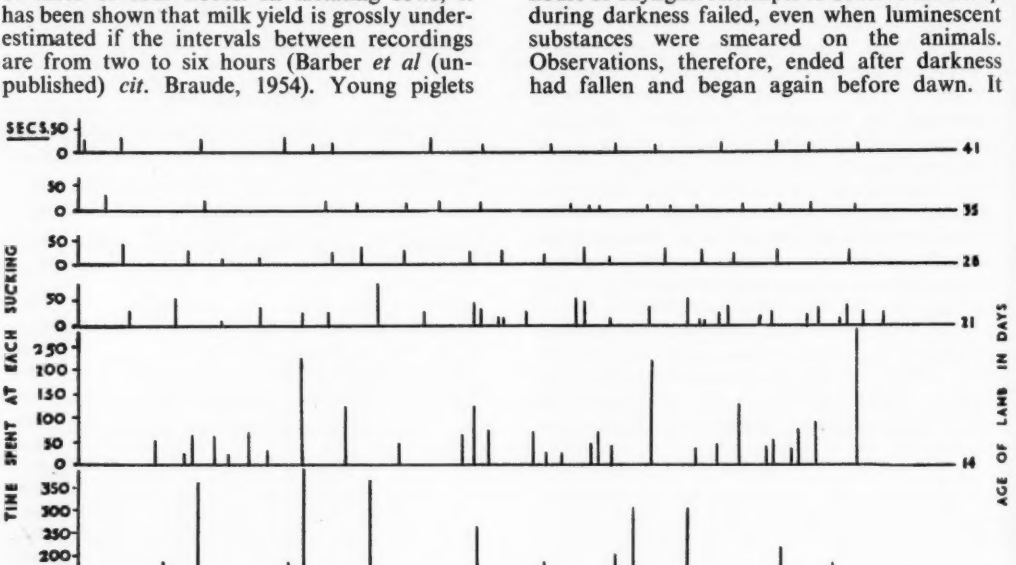

Fig. 1. Sucking behaviour of a twin lamb.

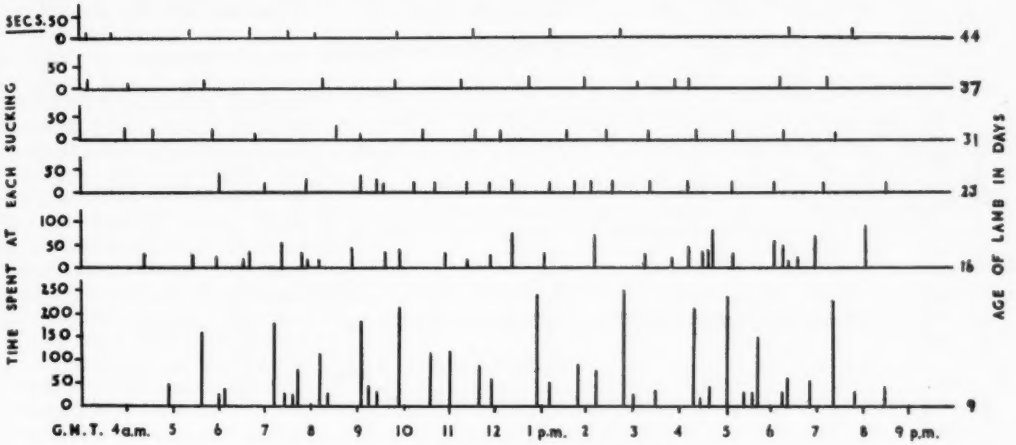

Fig. 2. Sucking behaviour of a twin lamb.

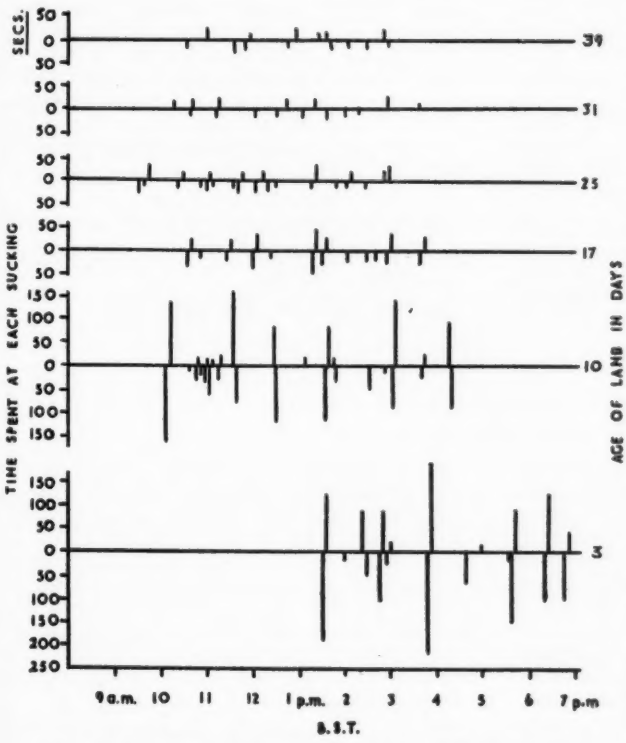

Fig. 3. Sucking behaviour of a single lamb from each side of the ewe.

of 6 hours (continuous observation) each week.

The times taken by the lambs at suckling were always recorded and in the case of single lambs the side of the ewe from which the lamb suckled.

Results and Discussion

Over periods of 16 hours' observation it was found that twin lambs suckled or attempted to suckle 15 to 45 times. Single lambs observed for periods of 6 hours suckled or attempted to suckle 9 to 25 times. In no case was the interval between sucklings as long as 4 hours.

It was noted that very young lambs were allowed to suckle by their dams at any time and for any length of time, but as the lambs grew older the ewes controlled the length of the suckling period by walking away and sometimes walked away without permitting the lambs to suckle at all. Generally, the lambs were allowed to complete a suckling within a few minutes of an unsuccessful attempt, but this was not invariably the case. The figures show the times and duration of successful suckling periods. These figures indicate that, as the lamb grows older, the time spent in

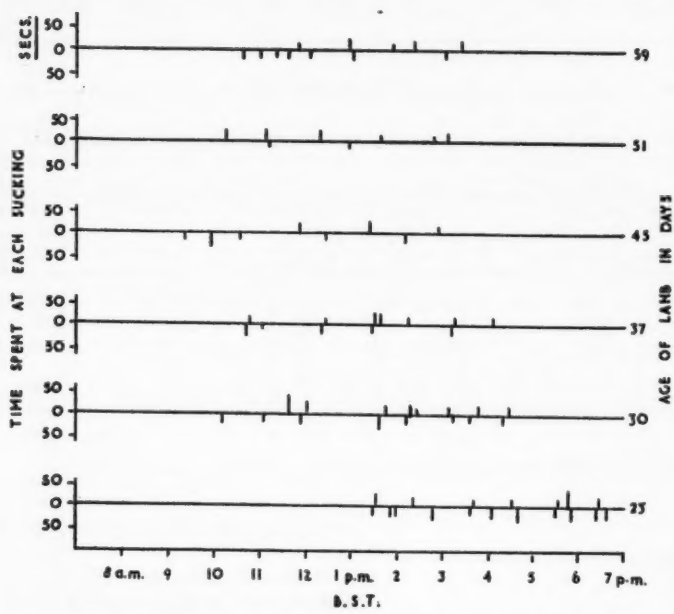

Fig. 4. Sucking behaviour of a single lamb from each side of the ewe.

suckling is decreased. This is due to the shorter duration and reduced frequency of suckling.

Observations on the suckling frequency of lambs were made by Barnicoat, Logan & Grant (1949) who wrote that lambs of 4-6 weeks of age suckled only about 6 times daily unless disturbed. In the present investigation, the minimum number of completed sucklings in 16 hours was 11 and the maximum 40. Barnicoat,*et al.* (1949) stressed that the external stimulus of suckling was more important than prenatal influences as twin-bearing ewes rearing single lambs yielded on the average, no more milk than single-bearing ewes. If sucklings are limited to 6 per day some of this stimulus may be lost and the milk yield of the ewe may be underestimated. In addition, more freqeunt suckling by the lamb would decrease back pressure in the udder and give a greater milk flow.

Summary

Under natural conditions, twin lambs up to 6 weeks old, suckled on average 22 times in 16 daylight hours. Single lambs suckled on average 14 times in 6 daylight hours. The duration of suckling periods became shorter and less frequent as the lambs grew older.

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PROCEEDINGS OF THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR

A two day meeting of the Association was held in Cambridge on 11th and 12th July, 1955. The programme on the first day included visits to the Department of Experimental Psychology in the morning, and to the Department of Zoology, the A.R.C. Unit of Reproductive Physiology, and the Ornithological Field Station, Madingley, in the afternoon. The proceedings on the second day took the form of a symposium on "abnormal behaviour" with the President, Dr. N. Tinbergen, in the chair. The following papers were read.

THE EFFECTS OF INSEMINATION ON THE BEHAVIOUR OF FEMALE *Drosophila subobscura*, AND SOME EFFECTS OF INBREEDING ON MALE BEHAVIOUR

By J. MAYNARD SMITH

Department of Zoology, University College, London

Drosophila subobscura females which have copulated and have been inseminated rarely remate, even if tested two or three months later when there is no longer sperm present in their receptacles. However, females which have copulated with testis-less males whose accessory glands, ducts and external genitalia are normal, or with males which have exhausted their sperm in previous matings, readily remate 24 hours later. It follows that it is the fact of having been inseminated, and not the act of copulation, which alters a female so that she does not remate, and that her changed behaviour persists even when she no longer contains stored sperm.

The mating success of outbred males is higher than the success of inbred males, as measured by the proportion observed to copulate within one hour of pairing with outbred females. Male success is not greatly affected by the presence or absence of testes. Inbred males usually court with high intensity, but do not accurately follow the rapid side-to-side movements of the female during the courtship dance; the failure of inbred males is due to low athletic ability, and not to low sexual drive.

Females mated by outbred males leave approximately four times as many offspring as those mated by inbred males. There is thus a correlation between the mating success, athletic ability and fertility of the males studied. If a similar correlation exists in wild populations, the courtship movements of a female will confer selective advantage in ensuring that she mates with a fertile male. If so, these movements may have evolved under the influence of sexual selection of the kind postulated by Darwin.

ABNORMAL BREATHING BEHAVIOUR IN A FISH

By J. B. S. HALDANE and H. SPURWAY

Department of Biometry, University of London

"It is hardly possible to exaggerate the importance of miscarrying behaviour patterns as a source of our knowledge" (Lorenz). We suggest that gross irregularity in a time sequence of normal acts is one criterion of such miscarriage. This can be estimated quantitatively and objectively, and used for comparison.

When *Anabas testudineus* breathes a series of gas mixtures in which the oxygen varies from 100 per cent. to 7 per cent., the mean interval between ascents to breathe is roughly proportional to the amount of oxygen. But the coefficient of variation (standard deviation divided by mean) remains at about .25. That is to say the ascents are only moderately irregular .When it is mechanically prevented from reaching air it may stay down for long periods. In both circumstances incomplete ascents and descents, which may be regarded as intention movements, are rare.

But when the fish breathes nitrogen or oil, the exteroceptive releasing and perhaps consummatory stimulus is not followed by a proprioceptive consummatory stimulus, and abnormal behaviour results. After a number of ascents in rapid succession the fish settles down to a behaviour pattern where the longest

interval between ascents may be over fifty times the shortest. The mean remains within normal limits, but the coefficient of variation is about 1.5, that is to say the timing is grossly irregular. Incomplete ascents and descents are also common, so qualitatively new elements are interpolated into the pattern.

Penrose has described similar phenomena in human psychotics, and they occur in morphogenesis as a result of disease, inbreeding and hybridity. Such irregularities can easily be measured in "spontaneous" activities, and may often be a useful objective indication of abnormality.

DISPLACEMENT ACTIVITIES—A RE-EXAMINATION OF THE PROBLEM

By N. TINBERGEN

Department of Zoology and Comparative Anatomy, Oxford.

No précis of this paper was available at the time of going to press.

"DISPLACEMENT" BEHAVIOUR AND "PSYCHOSOMATIC" DISORDER

By S. A. BARNETT

Department of Zoology, Glasgow

Displacement behaviour is the performance of an activity, in biologically inappropriate circumstances, when the appropriate action is prevented or the input to the C.N.S. departs from an optimum. Such behaviour may thus arise, not only from failure to perform or to complete a consummatory act, but also from the absence of a "consummatory situation". It is suggested that the sensory aspect is the more fundamental, since an activity is accompanied by a proprioceptive (and interoceptive) input, and this is presumably responsible for the cessation of activity once a consummatory act has been performed.

In human behaviour there is an almost complete absence of "innate" behaviour in the sense of stereotyped reaction patterns. Human behaviour of the kind which is said to arise from "instinct" is infinitely variable (apart from reflexes) on the motor side; but it tends to achieve particular afferent inputs (consummatory situations), such as a full belly or a particular skin temperature. If such ends are not attained, behaviour may be disturbed: "psychoneurotic" behaviour, e.g. in hysteria or obsessional states, is analogous in certain respects to displacement behaviour in birds or fish. Psychoneurotic behaviour is, however, not "innate", but in a sense learnt. In this it resembles, for example, the behaviour fixations developed by rats in frustrating situations.

In all these examples one motor output is substituted for another. The same applies in the "psychosomatic" disorders of man, in which an autonomic discharge, resulting from some form of "stress", produces a disorder such as asthma. It is suggested that the distinction between psychoneurotic and psychosomatic disorder is unjustified; that both might properly be called "neurotic" or "neurogenic"; and that the distinction arises from a conventional mind-body dualism which is now a handicap in the interpretation of behaviour.

It is further suggested that displacement behaviour and neurotic responses of all kinds may represent a general feature of the functioning of nervous systems: namely, that if there is an excitatory state which would ordinarily produce a motor discharge; and if the motor output cannot take its "normal" form; then it will follow some other pattern. This proposal may be regarded as an hypothesis. It urgently requires investigation and clarification by neurophysiologists.

In general, there is need for more effective communication between ethologists, psychologists, physiologists and psychiatrists, and for the development of research in which physiologists and students of behaviour combine. Given such collaboration, it should be possible to devise experimental programmes which would lead to a rapid advance in the understanding of behaviour.

(A fuller version has appeared in *The Lancet*, 1955, 2, 1203-1208.)

THE CONCEPT OF DISPLACEMENT ACTIVITY IN PSYCHOPATHOLOGY

By D. RUSSELL DAVIS

Psychological Laboratory, Cambridge

Psychologists as different in their other views as Freud and Tolman have resorted to concepts like that of displacement activity and have explained *out-of-context* behaviour observed in human subjects as being *derivative* or *substitute* activities resulting from frustration of adaptive behaviour. Several forms of behaviour observed in patients seem to be properly so explained, notably the masturbation and *compensatory* overeating of anxious children, and the laughter observed in hebephrenia.

So to explain inappropriate behaviours has the advantage that it specifies the conditions under which they occur, but it has also disadvantages. (i) The neurophysiological mechanisms are speculative. (ii) The concept of displacement suggests that these activities are homeostatic, whereas clinical observation suggests that they are not. (iii) The context in human patients is difficult to define, and it is not therefore easy to say what is and what is not out of context. (iv) Little or nothing is known about the factors which decide the channels of the vicarious discharge of excitation. (v) Other psychopathological explanations, depending largely upon learning theory, attempt to define the reward which reinforces apparently inappropriate behaviour.

However, symptoms may be provisionally classified as displacement activities if (i) they persist to a degree out of proportion to the gratification they achieve, (ii) they follow patterns little modified through the processes of learning, and (iii) they are so "incomplete, eccentric and imperfectly oriented" that they are ineffective in achieving gratification.

THE VARIETIES OF HUMAN CONFLICT AND FRUSTRATION AND THEIR CONSEQUENCES

By B. M. FOSS

Department of Psychology, Birkbeck College, London

Of the various criteria used for deciding if human behaviour is "abnormal," two extremes exist: conformity to a cultural norm, and individual "mental health." Some effects of conflict and frustration would count as "normal" for both criteria, others "normal" for one only, and still others as "abnormal" for both. In this paper, the results of conflict and frustration are classified without considering their possible "normality/abnormality."

Conflict and frustration situations can be classified according to (i) antecedent conditions; (ii) consequent behaviour; (iii) physiological mechanisms brought into play by the situations. (Some kinds of consequent behaviour can be identified as being "out of context," other kinds not). It is considered that very few human activities would be classed with displacement activities in all three of these classifications. Those which do resemble displacement activities are *not* generally labelled either "symptoms" or "abnormal." "Symptoms" are seen as arising from stress situations rather than from temporary conflict. However, a detailed investigation of displacement activities may throw light on the "choice of symptom" resulting from stress.

Production and a Pelagic Fishery

by D. H. CUSHING

Principal Scientific Officer, Fisheries Laboratory, Lowestoft

Factors which govern shoal aggregation of fish in areas where they can conveniently be caught are largely unknown. The summer shoaling of herring in the North Sea appears to afford a profitable field for the study of these factors. In this monograph Dr. Cushing discusses data on the occurrence of planktonic organisms on which pelagic fish are known to feed, and their relation with their predators and with one another. The data were gathered during a series of North Sea cruises in 1949.

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SOME REMARKS ON BEHAVIOUR IN CONFLICT SITUATIONS, WITH SPECIAL REFERENCE TO *Emberiza* Spp.

By R. J. ANDREW

Madingley Ornithological Field Station, Department of Zoology, University of Cambridge

For much of their waking life animals have simultaneous tendencies* to act in different and incompatible ways. Tinbergen (1952) and others, have shown that behaviour in such "conflict-situations" sometimes consists of a mixture of components, some of which express one tendency and some the other ("ambivalent" behaviour), or of apparently irrelevant behaviour which expresses none of the tendencies obviously present ("displacement activities").

This paper is intended to make three points concerning the behaviour given in conflict situations:

1. A description of a conflict-situation, where possible, should specify which responses are incompatible instead of stating, for instance, that fear and aggression† are conflicting.

2. The terms available for the description of behaviour in conflict-situations are not adequate. The term "compromise behaviour" is suggested for behaviour which can express both simultaneously present tendencies.

3. Displacement activities are often said to be caused by "sparking over" of motivation (e.g., Tinbergen, 1952; Bastock, Morris & Moynihan, 1953). Hinde (in press) has shown that this is an explanation only in terms of the hydraulic or electrical model which has often been used to depict the causation of behaviour. It is suggested here that certain apparently irrelevant behaviour may be caused by the same factors as in its normal functional occurrences.

I. Responses which are Incompatible

Conflict-situations are usually said to involve incompatibility between tendencies to give groups of responses, such as fear and aggression (Tinbergen, 1952; Hinde, 1952). It is, however, often both more accurate and more useful in predicting behaviour to say that tendencies to give two groups of responses are present, and that some of the responses of each group are incompatible‡ with some of the other. This can best be exemplified by showing that the incompatibility between two responses does not depend on the tendencies they express.

The conflict-situations discussed here are those which give rise to intention movements of flight (see Daanje, 1950; and Andrew, in prep., for descriptions of these patterns). These movements occur when a tendency to fly is accompanied by a tendency to give some incompatible response (which may be a tendency to remain still). Certain *Emberiza* spp. (British Buntings) flick their tails (a common passerine intention movement of flight) frequently as they move through twigs but only rarely as they move on the ground (Table I, and Andrew, in prep.). The relevant difference between the two situations is that flight is rarely used in moving on the ground, where hopping and walking are the

Table I. The Mean number of Tail Flicks Given in 15 seconds by *Emberiza* spp. The bird was unalarmed and moved continuously in the 15 second periods used in the calculation of this Table. A *t*-test was used to compare the situations for each species.

	E. schoeniclus	*E. calandra*	*E. citrinella*
Moving on ground	2.5	0.75	0.65
Moving through twigs	19	2.6	2.6
Significance of difference between the two situations	p.<.001	p.<.001	p. .05—.02

*The term tendency is used to avoid the ambiguities of the term "drive," following Hinde (1955, and in press).

†Fear and aggression are used in the sense of tendencies to give certain groups of responses. Fear responses include fleeing, hiding, freezing, etc.

‡Two responses are said to be incompatible in a particular situation when, although their casual factors are simultaneously present, they never occur together: it is not implied that incompatibility is mechanical alone.

principal types of locomotion, but frequently in moving through twigs. *E. schoeniclus* for instance often flicks its tail repeatedly as it sidles along a twig between flights; the tail flicks are thus given when the bird has simultaneous tendencies to move by flight and by sidling, which in this environment are almost equally strong. In the unalarmed birds on which these observations were made, the incompatible locomotory responses both express the same tendency to give a group of responses (e.g. to feed).

Tail flicks also occur when tendencies to give two different groups of responses are simul taneously present. Thus a hungry *E. citrinella* perched near a food dish at which a feared superior is feeding, elongates its neck and may raise its crest (fear responses, Andrew, in prep.), sometimes rubs its mandibles together in de-husking movements (a feeding response), and flicks its tail. Fear and feeding are thus ex pressed in certain responses which are compatible, but each would be expressed, in the absence of the other, by responses which are here incompatible; that is, flying away (fear) and flying towards the dish (feeding). In both this and the conflict situations described in the previous paragraph, the essential incompatibility is between two locomotory movements, one at least of which involves flight, and it is not surprising that the same behaviour (tail flicking) is given in both. In the case of the hungry bird, tail flicks, because they express a tendency to fly without involving any displacement of the body, can express both tendencies although these are to fly in different directions (*cf.* below).

II. Responses which can Express Two Simultaneous Tendencies

In some conflict-situations a response is given that resembles in form responses depending on both the simultaneously present tendencies. The term "Compromise behaviour" is suggested for such behaviour. Compromise behaviour differs from ambivalent behaviour in that it does not consists of a compound behaviour pattern, some components of which express one tendency and some the other, but of a single behaviour pattern or component which can express both. It is not always possible to distinguish strictly between these two types of behaviour (see below).

The tail flicking given by the hungry bird described in the previous section is an example of compromise behaviour; three further examples are described briefly below (see also Andrew, in prep.).

1. A male or female *Emberiza calandra* on first meeting its mate after an interval may give either "courtship wing vibration" (indicative of a sexual tendency, Andrew, in prep.), or, sometimes, "feather settling movements" (i.e., body shaking, wing vibration, fluffing, etc.). The feather settling movements, which are apparently irrelevant, include much more marked wing vibration than do "relevant" feather settling movements given with dry wings. Thus the feather settling is altered by the emphasis of that component which can also express the sexual tendency.

2. There is evidence in *Emberiza* spp., that the male and female sexual responses share certain short term causal factors (as well as differing in others). This may be summarised as follows (see also Andrew, in prep., and cf. Hinde, 1955)

(*a*) Both are aroused by the presence of the mate and may be expressed in similar behavioural components (e.g. wing quivering in *E. calandra*).

(*b*) Both are associated with the carrying of nest material (e.g. both male and female sometimes carry nest material during, or immediately after certain courtship displays, or on encountering a mate).

(*c*) Under certain circumstances a male *E. citrinella* with a strong sexual tendency solicits (a female response), and a female, also with a strong sexual tendency, responds to this behaviour as would a male, by attempting to mount and copulate (Andrew, in prep.).

(*d*) It is probably relevant that male and female behaviour patterns in general also share long term causal factors (e.g. both are made more easy to arouse by the same hormone, although to different extents), (see Hinde, 1955 for review of evidence from the literature).

Thus a sexual tendency may be expressed by responses appropriate to either sex, but normally males give male, and females female responses.

Male soliciting in *E. cintrinella* is an example of compromise behaviour. A male only solicits immediately after it has broken off a copulation attempt by flying down from the female's back; immediately after soliciting, it usually attempts to copulate again (such soliciting occurred in 15/110 fully observed attempted copulations in the field). There is little doubt, then, that the male has a strong sexual tendency whilst he solicits. Copulation attempts are usually broken

off because of increasing fear of the female (Andrew, in prep.; cf *Chloris chloris*, Hinde, 1954). Thus males solicit whilst they have a strong sexual tendency, which would normally be expressed in approaching the female to copulate, and fear of the female strong enough to prevent any such approach. Soliciting, expresses the sexual tendency and yet, as it is always a stationary display, permits the male to avoid the female and so is compatible with strong fear of her.

Soliciting by male passerines has been described in a number of other species (e.g. *Carduelis carduelis*, Conder, 1948; various Carduelines, Hinde, 1954, 1955; *Poephila guttata* Morris, 1954). Morris also emphasised the conflict between fear and sexual tendencies but explained the soliciting as due to "spark over." The present explanation differs only in showing that soliciting by the male *E. citrinella* is compromise behaviour; and in pointing out that male and female behaviour have common short term causal factors, and that the appearance of the one, when causal factors for the other are present, need not be thought of as a "sparking over" of motivation.

3. A third example demonstrates the way in which compromise behaviour intergrades with ambivalent behaviour. (The full data are given in Andrew, in prep.). *E. schoeniclus* gives a note "eee" during flights, which expresses fear and is usually single, and also a soliciting call "titi - -" which expresses a strong sexual tendency. The female of a breeding pair often solicits when attacked by her mate. As she flies down from an attack in flight she often gives single "eee" notes. Sometimes instead she gives a rapid call "see-see - -", or the "eee" notes may turn into this call, which in its turn becomes the "titi" soliciting call, just before she lands and solicits. There is thus a change from a tendency to give "eee" notes (expressing fear) to a tendency to give "titi" (expressing the sexual tendency). The call given at this changeover has the rapid repetition of the soliciting call but the individual notes resemble "eee notes. It is a matter of semantics whether these two characteristics of the call be regarded as separate components and the call termed ambivalent behaviour, or the call be regarded as a single pattern and termed compromise behaviour.

III. Irrelevant Behaviour

Tinbergen (1952) emphasises that the chief distinguishing feature of displacement activities is their irrelevance, but defines them more stringently as "an activity belonging to the executive motor pattern of an instinct other than the instinct(s) activated. It is suggested here, however, that much apparently irrelevant behaviour occurs in response to the same stimuli as in its "relevant" occurrences. The temperature regulatory responses and drinking of *Emberiza* spp. during fear are taken as examples.

1. *Normal Cooling Responses.* No detailed information appears to be available In the cooling responses of passerines: Stresemann (1927-34, p. 204) notes that birds gape and breathe forcibly from the cervical air sacs when over heated.

Experiments were therefore carried out in which individuals of *Emberiza* spp. were exposed to heated air in a lagged cage with an observation hole at one side. The air came from a heater invisible to the birds and was at 75°; the temperature to which the birds were exposed was lower than this, since they sought out cool places. Each heating lasted about 5 minutes and the cooling responses appeared within the first two or three minutes usually whilst the bird was perched, quite unalarmed. (There was, therefore, no doubt that the responses were due to heat and not to fear). Four *Emberiza citrinella*, three *E. calandra* and one *E. schoeniclus* were used, each being tested twice. The responses of all species were fairly similar. The bird first gaped briefly and repeatedly, sometimes breathing out audibly at the same time. The gapes soon became almost continuous and the mouth was licked, no doubt because it had been dried by evaporation (cf. mouth licking below). The body feathers were now progressively sleeked, always most markedly on the belly, and the wings began to be raised without any extension at the wrist, in a characteristic way. *E. calandra* repeatedly moved the raised wings up and down slightly every 1-2 seconds (Fig. 1). Panting movements of the breast sometimes occurred.

Fig. 1.

Cooling thus seems to be effected by the evaporation of water from the respiratory passages and mouth. The sleeking of the feathers would reduce their insulating effect whilst the raising of the wings may permit heat loss in the axillary region from the large vessels to the pectoral muscles. The wing movements of *E. calandra* may set up air currents.

2. *Cooling Responses During Fear. E. citrinella E. calandra, E. schoeniclus, E. tahapisi goslingi, E. bruniceps* and *Plectrophenax nivalis* all show full cooling responses exactly similar to those described above, after fleeing about their cages. *E. calandra* (and *E. bruniceps*) repeatedly raise and lower the wings but *E. citrinella* do not, just as in the normal cooling of these species. The response is probably widespread in passerines: Nice (1943) stated that *Melospiza melodia* gape in similar circumstances. At the highest intensities, *Emberiza spp.* abandon the normal perching posture and lie gaping and panting with closed eyes.

It might be argued that the cooling responses are due to the muscular exertion of fleeing. A consideration of the cooling responses given by males of *Emberiza* spp. after sexual chases, however, makes this explanation unlikely. In the chases of *E. calandra* in the field, the male followed the female very closely and so went through the same exertions as she: she showed little fear of him and turned to fly with him as soon as he stopped chasing, but before and after chases he showed his usual fear of her, that is, he avoided or only hesitantly approached her (Andrew, in prep.). In 30/36 cases when the male was watched after a chase, he showed cooling responses, but the female never did (0/7 cases), ($p = < .001$ for the difference). In *E. citrinella* and *E. schoeniclus* (Howard, 1929) and *Plectrophenax nivalis* (Tinbergen, 1939) the male gapes after sexual chases but the female does not.

The evidence from attacks made by the male of a caged breeding pair on the female is conclusive on this point. In these pairs the males were inferior to the females in aggressive relations (Andrew, in prep., and cf. Hinde, 1953, on *Fringilla coelebs*) and the attacks were made despite strong fear of the female. Immediately after such attacks which involved hardly any physical exertion, male *E. bruniceps, E. calandra* and *E. citrinella* often showed the full cooling responses of the species.

Sweating, and probably hot flushes, are autonomic cooling responses which occur in man during fear.

3. *Warming Responses in Fear. Emberiza* spp. raise the feathers moderately and often assume a resting attitude when cold (or ill). (Such a moderate raising increases the insulation of the body: extreme in raising which the feather tips are separated would reduce it.). The same behaviour may be given during fear (Andrew, in prep.). Occasionally they tremble in fear (a movement which produces heat by muscular contraction. Trembling in fear also occurs in mammals (man, horse and dog).

4. *Possible Causation of Heat Regulatory Responses in Fear.* In mammals (man) superficial blood vessels are commonly constricted in fear as a result of sympathetic activity and this may be accompanied by a fall in skin temperature (Lindsley, 1951, p. 477). If this is the case also in birds, then a single hypothesis would tentatively explain the occurrence of heat regulatory responses during fear in both mammals and birds. Cooling during the constriction of superficial blood vessels may stimulate temperature receptors and so evoke warming responses. The later return of these blood vessels to normal may warm temperature receptors after their adaptation to a lower temperature, and so arouse cooling responses.

On this hypothesis, warming responses should appear very soon after fear has been aroused and cooling responses after a short interval. This is in fact the case in *Emberiza* spp. Resting attitudes and feather raising may appear very soon after fear has been aroused and, if they do, are often maintained for all the time it continues, (see Andrew, in prep., where the submissive function of resting attitudes, Hinde, 1952, is also discussed). Cooling responses, in contrast, tend to appear after other fear responses, often with a slight lag. Often a male *E. calandra* or *E. bruniceps* lands in a normal attitude from a sexual chase or attack, and then cooling responses slowly appear. In these species, they tend to persist through the courtship behaviour which often follows, without obviously interfering with it (Andrew, in prep.). Analysis of sequences of courtship behaviour in male *E. calandra* showed that cooling responses followed attacks on the female significantly often and persisted significantly often whilst other behaviour changed twice. (The method of analysis and the data, are given in Andrew, in prep.; the level of significance was taken as a deviation

of 2.6 times the estimated standard error). Such persistence and independence of other fear responses would be expected if the indirect causation suggested here were correct.

5. *Drinking in Fear. Emberiza* spp. often lick the mouth during protracted fear (sometimes the tongue tip can be seen, sometimes the licking must be deduced from throat movements). Similar dryness of the mouth occurs during fear in man (Lindsley, 1951, p. 468).

E. calandra sometimes drinks after gaping in fear, and a female *E. schoeniclus* which feared her mate drank on several occasions after copulating. It is likely that these and perhaps other examples of apparently irrelevant drinking during fear (Tinbergen, 1952) are stimulated by mouth dryness.

Summary

1. Conflict-situations are best described in terms of incompatibility between behaviour patterns (or components) that are simultaneously tending to occur. The incompatibility exists whatever the causation of the patterns in question. Conflict-situations giving intention movements of flight are taken as an example.

2. Sometimes two simultaneous tendencies can both be expressed in a single behaviour pattern or components; such behaviour may be termed "compromise behaviour." Four examples are given.

3. Some behaviour patterns that occur apparently irrelevantly, and so might be termed displacement activities, may be caused in the same way as in their normal functional occurrences. Cooling responses and certain other behaviour that is associated with fear in *Emberiza* spp. are discussed as possible esamples.

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I should like to thank Dr. W. H. Thorpe, Dr. R. A. Hinde and Dr. B. A. Cross for helpful discussion and criticism in the preparation of this paper.

Addendum

Since this paper was prepared two more papers have come to my notice.

1. Adrenalin may cause increased production of metabolic heat in mammals (Boothby & Sandiford, 1923). Possibly this sometimes raises the temperature of the whole body in fear.

2. Morris (in press) discusses the possible origin of display components from autonomic responses given in conflict situations, including amongst the latter, feather movements such as are given in temperature regulation.

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OBSERVATIONS ON THE BEHAVIOUR OF SUCKLING PIGS

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Of all domestic animals the newly-born piglet is probably the quickest to commence suckling and its behaviour from birth to weaning provides a most interesting study. Almost as soon as it is born the piglet finds a place on the udder and obtains milk, in some cases even before the severance of the umbilical cord and, by the time the complete litter is farrowed, it is actively competing for its place on the udder.

Donald (1937) and others have shown that the anterior teats normally produce most milk and, in general, the competition is for these teats. Braude (1948) and Barber, Braude & Mitchell (1955) have given some interesting details on pig behaviour under experimental conditions. The present paper corroborates some of their work and adds further observations concerning suckling pigs. We have used the term "nursing" for the act of the mother and "suckling" for the act of the young, in accordance with the recommendations of Cowie, Folley, Cross, Harris, Jacobsohn & Richardson (1951).

General Observations on Nursing and Suckling Behaviour

During parturition and for some hours afterwards milk is readily available, thus affording individual piglets the opportunity of suckling immediately they are born. Thereafter, milk ejection is a reflex process which is most probably stimulated through the massage of the udder by the complete litter. Nursing and suckling then follow a consistent behaviour pattern which can be divided into three parts—initial massage, milk ejection and final massage.

Initial Massage

The sow receives the piglets for suckling in a lying, or occasionally standing, position. Each piglet then massages around its respective teat with rapid upward and downward movements of the snout, during which time the sow grunts at slow, regular intervals. This initial massage stage lasts for about a minute, and ends when milk flow begins.

Milk Ejection

Towards the end of the initial massage period the mammary gland distends; concurrently the piglets get more excited and take frequent trial sucks. During the next few seconds the teats become erect; the milk begins to flow practically at once and the piglets hold the teats fully extended, appearing to swallow, at furious speed, rather than to suck. The milk flow appears to stop quite suddenly; the piglets then suck vigorously as if to draw the last drop, become quite excited, attempt to push one another away and, if a spare teat is within reach, suck it alternately with the regular one. During the period of milk flow the grunts of the sow are lower in tone though faster and often in quick runs of three or four, tapering from a high to a lower note—a contented and quite characteristic sound. As the flow stops so does the grunting. Frequently at this stage, one of the piglets, though not always the same one, will run round to its mother's nose and grunt excitedly.

Final Massage

This second massage by the piglets begins immediately it is apparent that there is no more milk to be had. It is much slower in rhythm than the initial massage and may continue for perhaps fifteen minutes, though normally it lasts for less than five minutes. During early lactation the final massage is terminated when the piglets fall asleep at the udder but, in later lactation, the sow brings it to an end by turning over on to her udder or by walking away.

Experiment

At the Rowett Institute experiments on the effect of ambient temperature on the growth of suckling pigs necessitated measuring, at every suckling, the amount of milk consumed by individual pigs in each of 8 litters. An opportunity was thus afforded to study their behaviour. Records were kept of (1) the positions adopted by the sows at nursing times, (2) the preference of the piglets for certain teats, (3) the time spent by the piglets on the massage of the udder both before and after actually removing milk, (4) the duration of the milk flow, and (5) the amount of milk consumed by each piglet at each suckling period.

For the first three days of life the piglets

Table I. Average Duration of Initial Massage, Milk-ejection and Final massage per Nursing for Seven Sows throughout Lactation

Weeks.	Sow							Average for all sows except A.
	A	B	1	3	4	5	6	
	Initial massage, average time per nursing (seconds)							
1.	—	56	—	—	—	—	48	—
2.	—	50	—	42	61	71	39	51
3.	78	41	60	40	59	79	36	52
4.	—	39	47	44	68	90	43	55
5.	—	38	51	45	81	108	56	64
6.	—	41	65	44	83	107	57	67
7.	116	47	52	41	71	108	62	63
8.	102	37	56	43	74	108	72	67
Average of all observations	—	41	55	43	72	97	52	60±9
	Milk ejection, average time per nursing (seconds)							
1.	—	15	—	—	—	—	20	—
2.	—	16	—	16	18	19	17	17
3.	16	17	18	16	16	17	15	17
4.	—	16	18	10	14	16	13	14
5.	—	16	15	9	13	15	12	13
6.	—	15	13	11	13	14	13	13
7.	15	15	12	12	13	14	14	13
8.	14	14	12	12	13	13	11	12
Average of all observations	—	16	15	12	14	15	14	14±0.5
	Final massage, average time per nursing (seconds)							
1.	—	200	—	—	—	—	188	—
2.	—	215	—	216	239	234	258	235
3.	139	208	128	186	134	195	193	178
4.	—	197	125	164	176	145	145	159
5.	—	180	71	177	122	136	125	126
6.	—	167	64	166	101	113	138	123
7.	74	163	46	166	138	110	126	122
8.	73	155	52	209	166	119	87	130
Average of all observations	—	185	78	180	149	146	156	149±16

remained with the sows. They had by then settled on their respective teats and numbers were reduced at random to 8 per sow. From the 3rd to 56th day of lactation they were housed apart from the sows and put to suck every one-and-a-half hours up to the 40th day and thereafter every two hours. The intervals imposed between sucklings were based on the average times observed in normal practice, though it is appreciated that these intervals are of an irregular pattern, particularly in the early stages.

Piglets were weighed individually before and after each suckling, and the difference between these weights was taken to be the amount of milk consumed. The piglets were roused a few minutes before the first weighing to allow time for defaecation and urination. Losses, between weighings, due to these causes were thus eliminated. The procedure proved extremely satisfactory, and the sows and piglets rapidly became adjusted to the routine.

Results

Table I shows the average duration of initial massage, milk-ejection and final massage. Out of some five thousand nursing periods there were only 13 occasions on which no milk was ejected.

The average time spent on initial massage was steady throughout lactation for litters 1 and 3; for litter B there was a tendency to spend less time as lactation proceeded, whilst litters 4, 5 and 6 spent an increasing time on initial massage up to the 5th week and levelled off thereafter. The time of actual milk-flow varied very little, and was surprisingly short at an average of 14 seconds for all sows. Between the second and the fourth week of lactation there was a definite decrease in the time spent by all litters on final massage, followed by a more gradual decrease and levelling off. It must be pointed out here that, under the conditions of the experiment, the piglets were removed from the sow when final massage was completed or at the end of five minutes on the infrequent occasions when this limit was reached.

The figures in Table II indicate that a direct correlation exists between the time spent on massage at each nursing and total milk yield. Although milk yield is mainly determined by other factors, it seems highly probably from these results, where the sows were housed and fed under identical conditions, that it is also influenced by massage. Sow 2 was a poor milker and went dry on her 21st day of lactation, and it is of interest to note that, up to this time, her piglets spent only 119 seconds on total massage per nursing compared with an average of 259 seconds for the piglets of the other sows over the same period.

Restricted Massage

When, at nursing times, a sow habitually lay on a particular side, the piglets suckling that side were restricted in the massage which they could give the udder. This restricted massage has apparently an affect on milk yield as is illustrated in the following examples. Sow A lay on her left side at all except 17 out of 754 nursings, and the four piglets on this side

Table II. Relationship Between Total Time Piglets Spent on Massaging the Udder at Each Nursing and Total Milk Yield 3rd-56th Day of Lactation

Sow	No. of observations	Average total time spent on massage at each nursing (sec.)	Milk Yield (lb.)
1	442	133	444.9
6	578	207	570.1
4	531	221	562.0*
3	570	223	606.9
B	571	227	621.0
5	587	244	766.6

*Not recorded during first 10 days, and 68 lb. have been added on the basis of the percentage of the total yields produced by the other sows during this period.

Sow A was observed less fequently and is excluded from this table.

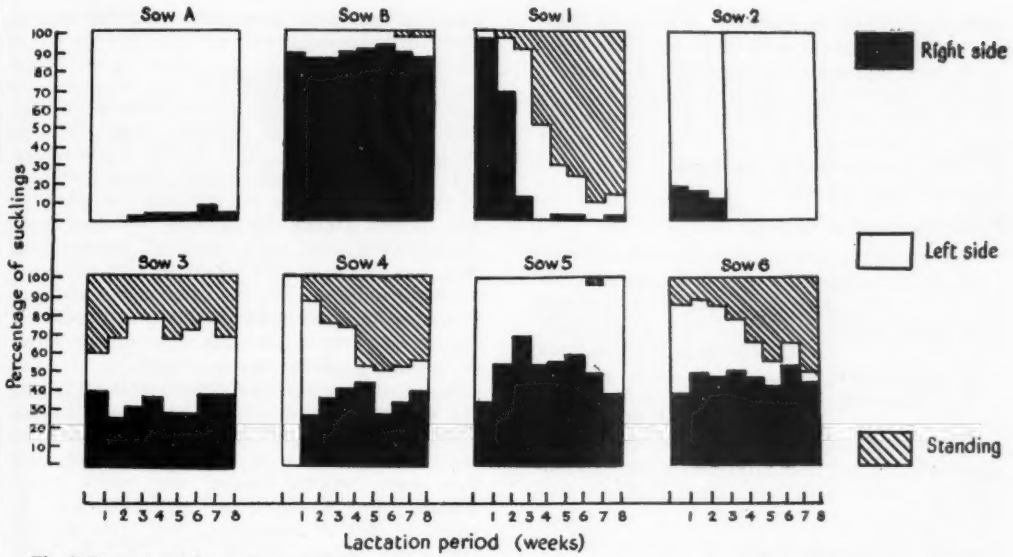

Fig. 1. Percentage of occasions on which each sow either lay on her right or left side or stood, at nursing times.

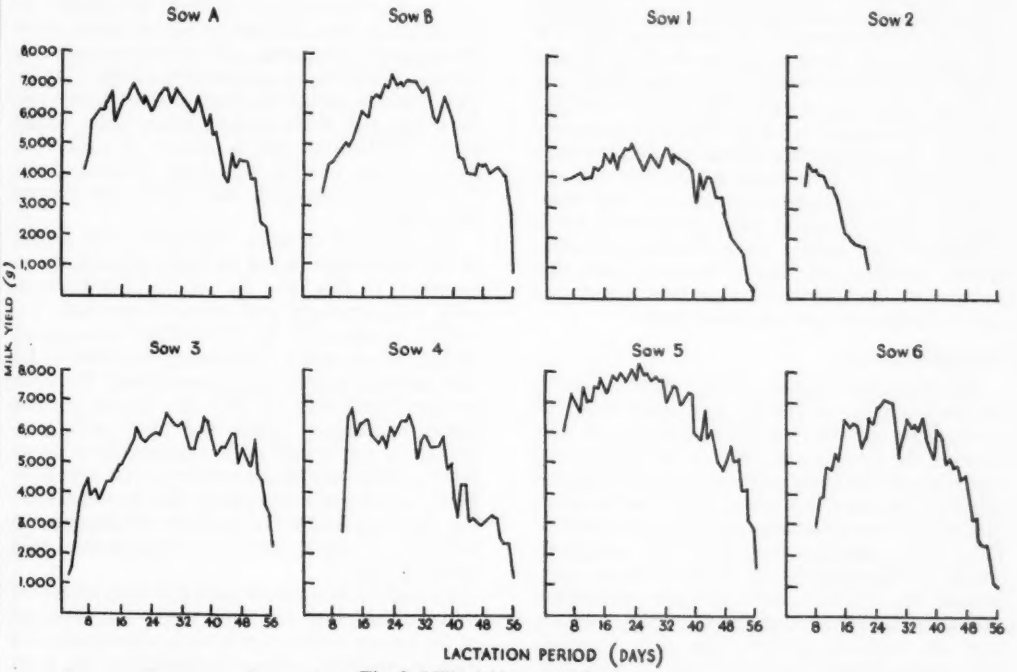

Fig. 2. Milk yield curves of sows.

(teats 1, 2, 3 and 4) got only 27.8 kg. of milk per piglet compared with 46.0 kg. per piglet for the four on the right side (teats 1, 4, 5 and 7). Sow B lay on her right side at all except 78 out of 744 nursings, and the three piglets on this side (teats 1, 3 and 4) got 31.5 kg. of milk per piglet whilst the five on the left side (teats 1, 2, 3, 5 and 7) got 37.5 kg. per piglet.

Position of Sow at Nursing

The remaining sows, although each followed a different behaviour pattern, lay approximately equal times on either side, and the percentage of nursings at which they lay on the right side, the left side, or stood, is given in Figure 1 for each week of lactation.

The piglets could not massage the udder so forcefully when the sow adopted a standing position at nursing time, and those sows which favoured this position produced a correspondingly lower total yield than those which favoured the lying position.

Anterior v. Posterior Teats

On the average, the 4 piglets of each litter which suckled from the teats nearest the anterior end of the udder got 15.3 per cent. more milk than the 4 nearest the posterior end. Of the 64 piglets in the 8 litters the 39 (61 per cent.) which suckled the 3 pairs of anterior teats got 83.8 per cent. more milk than the 25 (39 per cent.) which suckled the posterior 3 or 4 pairs of teats. These figures confirm the findings that the anterior teats are more productive and are suckled by more piglets than are the rear teats. Piglets which changed their preference for a particular teat during early lactation tended, where possible, to move towards the end anterior, though frequently an odd piglet was left to suckle the two rearmost teats.

Lactation Curves

The lactation curves of the sows (Fig. 2) are very similar in pattern and quite different from those of the cow or the sheep. In the case of the sow the curve rises steeply at the beginning of lactation and reaches its peak about the 20th day after farrowing. This level is maintained with some fluctuations for the next two or three weeks, and the yield then falls rapidly to weaning. The drops in the curves of some sows, around the 21st day, and the more precipitous drops for all sows around the 42nd day, coincide with the oestrous period. The daily nursings were reduced from 16 to 12 from the 41st day, and this may also have influenced the course of the drop in yield.

Discussion

Braude (1948) suggests that massage of the udder prior to milk ejection raises the fat content of the milk, and quotes Hammond's (1936) observation that, in cows, the composition of the milk depends on previous stimulation, and further quotes the findings of Ostertag & Zuntz (1908) that milk obtained by suckling pigs was twice as rich in fat as that obtained by hand milking. The final massage activity is probably an attempt by the piglets to induce a further let-down but, though this is unsuccessful, it probably does prove beneficial to the udder, and encourages optimum milk secretion. As has been shown, sows vary considerably in the time that they allow piglets to continue this massage. A sow, whose udder or teats may have become tender, will suffer initial massage and let-down but will turn over as soon as this is completed, and thus deprive the udder of any benefit from final massage. This effect emphasises the importance of the care of udder and teats.

The duration of milk-flow at an average of 14 seconds for all sows, varied very little throughout lactation, and bore no relation to the milk yield at any given nursing. Whittlestone (1953), using standard doses of oxytocic hormone for 6 Berkshire sows, also found little variation in the duration of milk-flow. The average time in his trials, however, was 27.5 seconds, nearly double that in the present experiment.

The amount of milk suckled by the piglets is the dominant factor in their growth up to weaning. In this trial the relationship between milk consumption and growth rate was $r = 0.9782$ based on 29 d.f. ($P < 0.001$). The amount of milk consumed varied greatly between litters and between piglets of the same litter. The sows yielded from 445 to 767 lb. during similar lactation periods, while the total milk consumed by individual piglets ranged from 20 to 100 lb. These variations may be partly genetical, partly nutritional and partly due to behaviour, but they emphasise the need for obtaining some measure of milk yield in experiments with suckling pigs.

In most trials the milk yield has been measured by recording one day each week. Examination of the figures in this experiment, where complete data is available, shows this method to be quite

sound. However, it must be remembered that, in the present instance, the piglets were accustomed to an unbroken routine of separation from the sow and to weighing before and after each feed throughout lactation whereas, in once a week recording, there may be errors due to upset of the routine of both sow and piglets. Further, when yields are estimated from one day a week recordings, care must be taken that the day chosen does not coincide with the oestrous period or an estimate below the true value will result.

Summary

1. The suckling behaviour of eight litters is described. The average duration of initial massage of the udder by the piglets, milk-ejection and final massage per nursing, for six complete lactations, was 60.5 sec., 14.2 sec. and 149.3 sec. respectively.

2. An apparent correlation was found between the total time spent on massage at each nursing and total milk yield.

3. The effect of the position adopted by the sows at nursing times on udder massage and milk yield is discussed.

4. Lactation curves of the sows were of a different shape from those of cows and sheep in that they reached their peak three weeks after parturition, remained at that level for a further three weeks and then fell rapidly.

5. Correlation between milk consumption and growth rate up to 19 days of age was 0.98.

6. The possible effects of the udder massage and the methods of recording yield are discussed.

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ON THE COURTSHIP BEHAVIOUR OF *Hypolimnas misippus* L., (Lepidoptera, Nymphalidae), WITH NOTES ON THE MIMETIC ASSOCIATION WITH *Danaus chrysippus* L., (Lepidoptera, Danaidae)

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Introduction

Hypolimnas misippus L., is a well-known mimic of the danaid butterfly, *Danaus chrysippus* L., and an account of the mimetism, together with coloured figures of the species concerned, may be found in Eltringham (1910) and Punnett (1915). Both species are widely distributed through the warmer countries of the Old World, and, although subject to considerable seasonal fluctuations in numbers, each may be regarded as being among the more abundant butterflies of the Achimota district.

Superficially the sexes of *D. chrysippus* are rather smaller, but in *H. misippus* there is a well-marked sexual dimorphism, only the females showing a mimetic resemblance to the danaid. The males of *H. misippus* show no resemblance either to their own females or to *D. chrysippus*. In Africa *D. chrysippus* occurs in three forms, but only one of these forms (*ab. alcippus*) is found at Achimota. Corresponding to the three forms of *D. chrysippus* there are three female forms of *H. misippus*, two of which are common at Achimota. The third form (*ab. alcippoides*, corresponding to *ab. alcippus* of the danaid) is characterised by the presence of a relatively large white area on the otherwise brown hind wing. This form does not occur at Achimota, although many specimens have a slight suffusion of white scales on the hindwing. Intermediate forms of *H. misippus* are frequent.

For a period of a few weeks during the latter part of 1954 *H. misippus* was unusually abundant, and the opportunity was taken to carry out some preliminary experimental work on the factors associated with the courtship of this butterfly. Observations on the behaviour of the males had previously suggested that the species would be particularly suitable for an investigation of this type. Furthermore, the extreme sexual dimorphism, and the mimetic resemblance of the female to another species of butterfly were both factors of added interest not present in *Eumenis semele* L., the courtship of which had been previously studied by Tinbergen, Meeuse, Boerema, & Varossieau (1942). In reviewing the experimental work to be described in this paper it will be apparent that certain obvious lines of investigation had to be ignored, and left for possible future consideration. It seemed undesirable, however, to delay publication of the results so far obtained, previous experience having indicated that it might be several years before the butterflies became again sufficiently abundant for the work to be continued.

The Wing Patterns of *H. misippus* and *D. chrysippus*.

The following brief descriptions are intended to supplement Figures 1 and 2.

H. misippus (female typical form) and *D. chrysippus* (typical form, both sexes). Fig. 2, *a* and *d*.

Ground colour of upper surface of wings a rich orange-brown. Costal border and apical area of forewings black, with a broken band of white traversing the black apical region. Hind wings with a black border.

H. misippus (female form *inaria*, Cram.) and *D. chrysippus* (form *dorippus*, Klug). Fig. 2, *b* and *e*.

Upper surfaces of wings a rich orange-brown to golden-yellow colour. Many of the specimens taken at Achimota had an apical pattern of darker and lighter brown scales that resembled in shape the black and white apical pattern of the typical female form.

H. misippus (female form *alcippoides*, Butl.) and *D. chrysippus* (form *alcippus*, Cr.). Fig. 2, *c* and *f*.

In both species the forewings are rather similar to those of the typical forms. On the hindwings, however, the brown coloration is almost entirely replaced by white, the latter extending almost up to the black border of the wing.

In specimens of *H. misippus* taken at Achimota the white area never covered more than a third of the total area of the hindwings. Normally, if white were present on the hindwing, it was

as a gentle suffusion of white scales over the area concerned, never as an extensive pure white area such as found in *D. chrysippus*. All the specimens of *D. chrysippus* seen at Achimota belonged to the form *alcippus*, and possessed conspicuous white hindwings.

The correspondence between the pattern of the undersides of the hindwings of the two species was rather closer than that of the upper surfaces, *H. misippus* developing rather more white on the underside than on the upper surface, while *D. chrysippus* developed rather less.

H. misippus (male). Fig. 1.

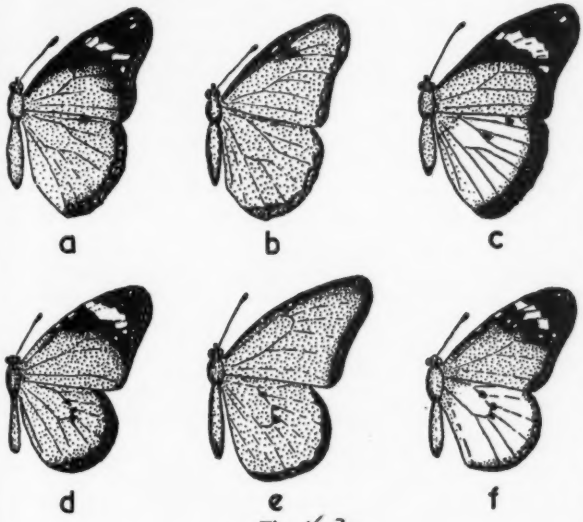

Fig. 1. 2

The upper surface wing pattern of the male *H. misippus* is simple, and quite unlike that of the female. The wings are mainly black, but in the centre of each wing there is a relatively large white patch. When viewed from a certain angle an iridescent blue area may also be seen in the centre of each wing, but these blue areas do not entirely correspond with the white patches.

Field Observations

That *H. misippus* would be a very suitable subject for experimental work on the mating behaviour of a butterfly was evident from two characteristic features of the male behaviour. These were a marked tendency to adopt a particular localised habitat, and an extreme readiness to investigate any other insect or bird that happened to fly past. In these respects it seems likely that the behaviour of the male *H. misippus* was somewhat similar to that of the male *Eumenis semele* studied by Tinbergen, Meeuse, Boerema & Varossieau (1942). Very frequently the males selected a particular patch of ground, or a stone, or a bush, where they were able to rest and sun themselves. From this observation post they darted out to investigate any other insects that flew past, generally returning to the same place when their investigation had been completed. Males that were in flight also tended to localise the area of their activities, flying to and fro over the same area of ground.

In their investigations of other flying creatures the males showed a certain degree of selectivity, probably related to the size, movement, and apparent colour or brightness of the other insect or bird. They almost invariably rose to examine any objects passing overhead, provided that the latter were not so small as probably to be invisible, or so large that they frightened the males away. There was, for example, a nearby colony of weaver birds that spent part of each day in the collection of nesting materials, and in so doing they passed back wards and forwards over an area particularly favoured by the *Hypolimnas* males. Although the birds flew at a height of some 15 to 20 feet above the ground they kept the butterflies below them in a constant state of activity, since the latter were continually rising in a series of futile attempts to follow the flying birds. The reactions of the males toobjects passing alongside them were dependant, at least some extent, on the brightness of the object to concerned. Large pale butterflies, such as *Pieris calypso* Drury and *Catopsilia florella* F., appeared to be of little interest to the *Hypolimnas* males; darker butterflies, however, especially those having a colour somewhat similar to that of the female *Hypolimnas*, were almost invariably investigated and frequently harried for some distance. It seems reasonable to suppose that such harrying as occurred was not necessarily of an aggressive nature, and that the sorties of the males were probably undertaken in order to find suitable mates.

The normal flight of the female *Hypolimnas* was slower than that of the males, and resembled

more the leisured flapping flight of the danaid. When disturbed, however, they were capable of a rapid and vigorous flight in order to escape.

Unfortunately, the complete behavioural sesequence of courtship and mating was not observed during the present series of observations. Temporary associations between the sexes were frequently seen, however, and since such associations gave rise to quite distinctive behaviour on the part of the male, it was assumed that such behaviour represented at least the beginning of the normal courtship sequence. One of the most characteristic features of this behaviour was a distinctive quivering flight, exhibited by both sexes, and in which, although the wings were vibrated with unusual rapidity, the actual speed of flight through the air was slow. During this quivering flight the body was held much more closely to the vertical than was the case during normal flight. This was particularly true of the females as they frequently appeared to hold their bodies completely vertical while carrying out the quivering flight.

The temporary associations between the sexes nearly always followed one of the two behaviour sequences now to be described.

When a male encountered a female in normal flight, it flew rapidly to her and in many instances actual physical contact occurred. The male then dropped so that it occupied a position some 3 to 6 inches below the female, and immediately commenced the quivering flight. The behaviour of the female was less constant but generally she also adopted the quivering flight, and the two would pass slowly over the herbage,—both quivering, and with the male flying below the female. Sooner or later, however, the female would start to rise slowly, but steeply, while the male followed immediately below her. These ascending flights frequently carried the butterflies up to a height of 30 to 40 feet, but in all of the many cases observed the male eventually broke off the pursuit, ceased the quivering flight, and dropped back rapidly to the ground. There was no evidence that, after the butterflies had descended, there was any tendency for the association to be resumed, other than by mere chance. On many occasions the female was seen to settle on the ground as soon as the male made his initial approach. The male then usually settled beside her, and both butterflies would pass into a state of comparative inactivity that might persist for some 5 to 10 minutes. During this period the butterflies generally remained still, with their wings closed above their backs. The female would occasionally flutter a few feet, but she was always closely followed by the male. This behaviour was never observed to terminate in the actual mating of the butterflies concerned. Normally the activity of the female reappeared after a few minutes, and she eventually terminated the association by rising in the ascending flight already described.

It may be noted here that, during the greater part of the day, males were seen far more frequently than were females. The latter appeared to fly for preference during a period of about two hours at mid-day, during which time they laid their eggs. At these times they were seen to be be as numerous as the males. A batch of nearly two hundred butterflies, reared from eggs, contained almost equal numbers of males and females. It seems, therefore, that the relative scarcity of the females at most times resulted from a difference in the behaviour of the sexes and not from a natural preponderance of males.

Experimental Methods

In the present series of experiments the object was to assay and compare the reactions of free-living *Hypolimnas* males when they were presented with various dead butterflies—hereafter referred to as "test insects." In order to standardise the conditions of the experiments the test insects were all prepared by a similar method and presented to the males in a similar fashion.

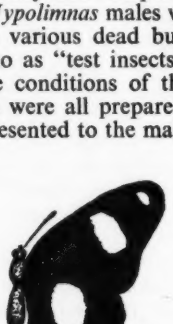

Fig. 2.

A test insect was prepared by cutting a groove across one of the flat faces of a small cork, and sticking the required butterfly body into this grove. The wings were then fixed onto the flat parts of the cork lying on either side of the groove, so that the completed test insect appeared to be in the normal "set" position, with the wings open and displaying the upper surface pattern. The various parts of the test insect were fixed to the cork by means of an adhesive, "Cow," a rubber gum made by P. B.

Cow & Co., Ltd., London, proving to be particularly suitable for this purpose. It was thus possible to prepare test insects that combined together the wings and bodies of the different sexes or species in any required combination. For the sake of consistency, however, the same procedure was used even when all the parts of the test insect came from the same original butterfly. The cork bearing the test insect was finally mounted on the end of a two-foot length of tensile wire the other end of which was attached to a six-foot bamboo cane. The resilience of the bamboo cane and tensile wire gave a more life-like movement to the test insect than would have been possible with a more rigid structure. Furthermore, by tapping the base of the bamboo cane, it was possible to set up a very rapid vibration of the test insect that simulated the quivering flight of the living female.

In all experiments an attempt was made to standardise the presentation and subsequent "behaviour" of the test insect. Essentially the idea was to manipulate the test insect so that its "behaviour" resembled as closely as possible that exhibited by the living females. The complete response of the male under these conditions could be divided into five definable, and numbered, stages. The reaction of any particular male was graded according to the number of the final stage that it achieved in the courtship sequence.

All tests in which the living male showed no response to the test insect were ignored as it was uncertain whether the lack of response had resulted from the failure of the test insect to stimulate the courtship sequence of the male, or from the failure of the male to see the test insect. In the course of the experiments described in this paper, instances in which the male showed no response to the test insect were rare.

Normally the test insect was moved past the living male at a distance of 2 to 3 feet, at a moderate speed, and with a gentle dancing motion to imitate the flight of the female. If the male merely flew to the test insect, gave it a cursory examination, and then flew away, the response was classed as a Grade 1 reaction. If, however, the male showed greater interest and followed the test insect for a short distance, the response was regarded as a Grade 2 reaction. In the appropriate circumstances, the male would then follow the test insect for a short distance, drop below it, and commence the quivering flight. Such a response was recorded as a Grade 3 reaction. As soon as the male commenced its quivering flight, the test butterfly was gently vibrated by tapping the base of the bamboo stick, and then taken gently to the ground. When a normal female test insect was being used the male frequently responded by settling on the ground beside it.

The subsequent procedure and the assessment of the Grade 4 and 5 reactions was changed during the course of the series of experiments, since the procedure adopted at first proved later to be unsuitable. In the first sets of experiments the male was credited with a Grade 4 reaction if it remained on the ground beside the test insect for at least five seconds, the test insect not being vibrated during this period. Finally, the vibrating test insect was raised slowly into the air to simulate the ascending flight of the living female, and if the male followed closely behind, quivering continuously, it was credited with a Grade 5 reaction.

In the later experiments the procedure was changed as it was noticed that many males, which appeared to be strongly attracted to the test insect, failed to follow the ascending flight, but passed instead into a state of catalepsis. This state endured for a minute or two during which time the males appeared to be quite insensitive to outside stimuli. Not only did they fail to follow the ascending flight of the test insect, but they could also be approached without undue care and picked up in the fingers. Following the procedure just described such males were credited with a Grade 4 reaction, which implied a weaker response than that given by males which had settled restlessly beside the test insect for five seconds and were then ready to follow the ascending (or any other) flight of the test insect. It seemed more reasonable to regard the catalepsis as being the more complete reaction, and as marking the end of the sequence of reactions that could be elicited by a suitable test insect. On a revised procedure, therefore, that was used in the later experiments, the ascending flight of the test insect was omitted, and the test insect was merely vibrated gently while on the ground. When the male had settled beside the test insect it was stroked a few times with the test insect, a process that had been found to encourage the catalepsis of the male. If the male settled, but remained active, it was given a Grade 4 reaction; if it passed into catalepsis it was given a Grade 5 reaction.

The actual significance of the catalepsis was uncertain, particularly as the complete courtship sequence had not been observed. It may have been that the cataleptic male was waiting for some further stimulus that would normally have been forthcoming from a living female. Alternatively it may have been a catalepsis that would normally have been associated with actual copulation—it is a frequent observation that during the copulation of butterflies, although one partner may remain active, the other frequently becomes completely inert and quiescent. The second explanation gained a further support from observations on males that succeeded in copulating with the test insects. Such males had not, of course, passed into a state of catalepsy prior to copulation, but they did so immediately after union with the female test insect had been achieved. Whichever of these explanations of the catalepsis is accepted, it still seems reasonable to regard it as the climax of the male courtship sequence.

The numerical grades finally accorded to the various responses of the male are tabulated in Table I.

Table I.

Reaction of male	Grade recorded
Rapid cursory inspection	1
Greater interest, indicated by tendency to follow	2
Quivering flight	3
Settling on ground for 5 seconds	4
Catalepsis	5

The distinction between reactions 1 and 2 was somewhat arbitrary. Many of the reactions classed as Grade 1 involved apparently only visual inspection, but this was not always the case. In the rapid darts that the males carried out to inspect the test insects it was often impossible to see how closely the male approached the test insect, and whether antennal contact would have been possible. Reactions 3, 4, and 5 were usually easy to define.

In presenting the results obtained by use of the first experimental procedure (i.e. that which incorporated a final ascending flight with the test insect) it was decided to include all the reactions 4 and 5 that had been obtained in a single group, and to quote them as a Grade 4 reaction. This overcame the criticism that some of the males credited only with a Grade 4 response were, in fact, responding more strongly (catalepsis) to the test insect than those credited with a Grade 5 reaction. In the present paper, therefore, the experiments utilising the first procedure may be recognised by the histograms, which only carry four grades of reaction.

In order to carry out any experimental test a walk was taken around the perimeter of a golf course at Achimota and the test insect was presented to any male *Hypolimnas* that were encountered *en route*. If a male showed a low-grade response (Grade 1 or 2) the test insedt was presented to it a second time if circumstances permitted. Since a male which gave a low-grade response to the first presentation tended to give a similar response to the second, and since the histograms record individual responses, it follows that the histograms tend to be somewhat biased in favour of the low-grade responses.

Experimental Results

(*a*) *The Attractive Properties of a Female Hypolimnas Test Insect.*

At the outset it was necessary to show that test insects prepared from freshly killed *Hypolimnas* females were attractive to the males, and also that their attractive properties did not deteriorate so rapidly as to complicate the interpretation of experiments carried out, say, during the course of a day.

A series of experiments indicated quite clearly that freshly killed females were normally attractive to the males, but that the attractive qualities were much reduced by prolonged storage or by oven drying. Under normal conditions of storage, however, there was no untoward diminution of the attractive properties over a period of a few days. The results obtained from one of these experiments are shown in Fig. 3, Experiment 1. For this experiment four female *Hypolimnas* were killed, and prepared as test insects in the standard fashion. In order to confirm that they were all attractive to males they were tested individually on the afternoon of the day on which they had been killed (first day). Test insects A and B were then over dried at 70°C. for 18 hours, while C and D were left at room temperature. The four specimens were again tested against the males on the afternoon of the next day (second day). Unfortunately, heavy clouds reduced the number of tests possible on

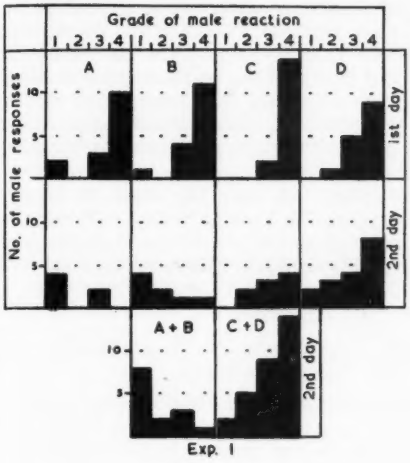

Fig. 3.

the second day, and in order to make the overall result apparent it is necessary to add together the responses obtained by the individuals of each pair. This has been done in Fig. 3, and it will be seen that the oven drying reduced the attractiveness of the females, probably by driving off some volatile secretion.

It will also be noted that the reduction in attractiveness was accompanied by a great increase in the proportion of grade 1 reactions obtained. This fact implied that this grade included many reactions in which the male had approached sufficiently close to the test insect to appreciate chemosensory stimuli, or the lack of them.

On one occasion a freshly killed female aas found to exercise little attraction over the males, the latter giving a series of low-grade responses (1 and 2). It may have been significant that the female concerned was very freshly emerged from the pupa. As a precaution, therefore, in later experiments freshly emerged females were avoided, and all females were tested before use to confirm that they possessed the necessary properties for attracting the *Hypolimnas* males.

(*b*) *The Effect of the Sex of the Individual Parts of a Test Insect in determining the Responses of the Male.*

A short series of experiments was carried out to assess the importance of the various parts of the female test insect in the induction of the courtship sequence of the male. In this series

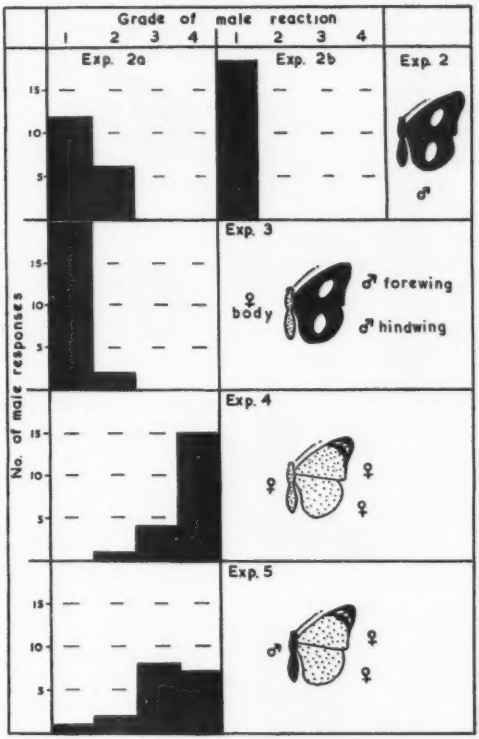

Fig. 4.

the effects of combining the body of one sex with the wings of the other were studied, and the results obtained are shown in Fig. 4, Experiments 2-5.

1. Combination of male body with male wings (Experiments 2a and 2b).

This combination reproduced the normal male butterfly, and it only obtained low-grade responses from the living males. Although living males tended to chase each other, and displayed a certain aggressive(?) type of behaviour, no such reactions could be provoked by the use of the male test insect. It was merely inspected, perhaps followed for a short distance, and then ignored.

2. Combination of male wings with female body (Experiment 3). The wings of the male test insect used in experiment 2b were combined with the body of a freshly killed female. The resulting test butterfly was treated as a male, evoking little interest from the living males.

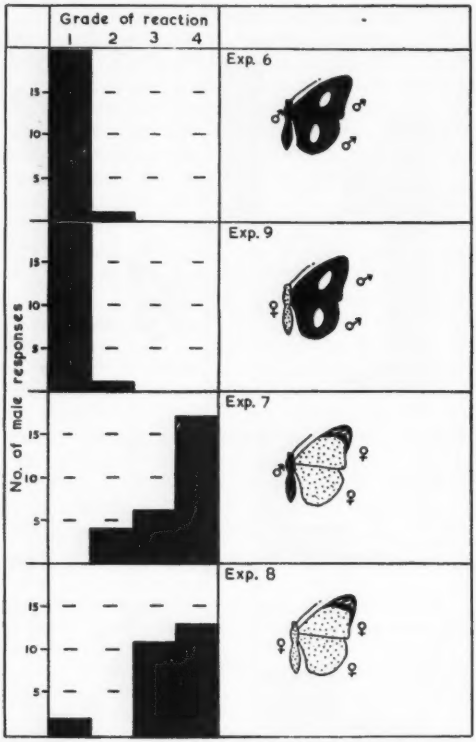

Fig. 5.

3. Combination of female wings with female body (Experiment 4). The female body of experiment 3 was fitted with the wings taken from a freshly killed female. This control experiment indicated that the combination of female body and female wings used in this series of experiments was suitably attractive to the males.

4. Combination of female wings with male body (Experiment 5). The female wings used in experiment 4 were combined with the male body used in experiment 2b. Living males responded to the resulting test insect as though it were a female, although the results suggested that the overall response was somewhat less complete than that obtained by the test female in experiment 4.

The results obtained in this series of experiments were confirmed by those obtained in a second series of similar experiments (Fig. 5, Experiments 6, 7, 8, and 9). They emphasised the dominant effect of the wings, as compared with the body, in determining the reactions of the male, and indicated that factors associated with the female wings were essential to the effective maintenance of the sequence of male courtship reactions. The presence of the male wings appeared to interpose a complete block to such maintenance at an early stage of the courtship sequence. If, however, female wings were present to take the male through the earlier responses there was some evidence that a complete reaction was obtained more readily with a female body than with a male body. The difference, however, was slight, and may not have been significant.

(*c*) *The Significance of Visual Stimuli arising from the Female Wings.*

Further experiment (Fig. 6, Experiment 10) showed that the presence of the scales on the female wings was an important factor in stimulating the courtship responses of the male, removal of the scales resulting in a great reduction in the intensity of these responses. In experiment 11 (Fig. 6) the female wings were replaced by paper wings which had been coloured in the normal female colours with Rowney's powder paints. The powder paints were applied with water, and since they themselves were unlikely to possess any odour,

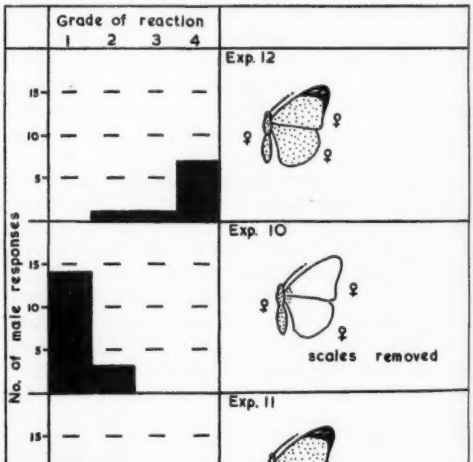

Fig. 6.

it is unlikely that the artificial wings supplied any stimuli other than visual ones. It will be seen from Fig. 6 that the test insect with the artificial wings and a female body obtained a stronger response from the males than the female from which the scales had been removed. The great increase in the proportion of males showing a Grade 2 response (18 per cent. in experiment 10, 55 per cent. in experiment 11) indicated the importance of visual stimuli in the production of this response. The fact that some *complete* responses were obtained indicates that the test butterfly with artificial wings possessed all the properties necessary to elicit such responses from the males, but possessed them to a lesser degree than did the normal female.

The results of experiments 10 and 11 may be interpreted thus:

1. The artificial wings possessed certain visible properties (e.g., perhaps a certain degree of brightness, colour, shape*) that were absent from the denuded wings and from the female body.

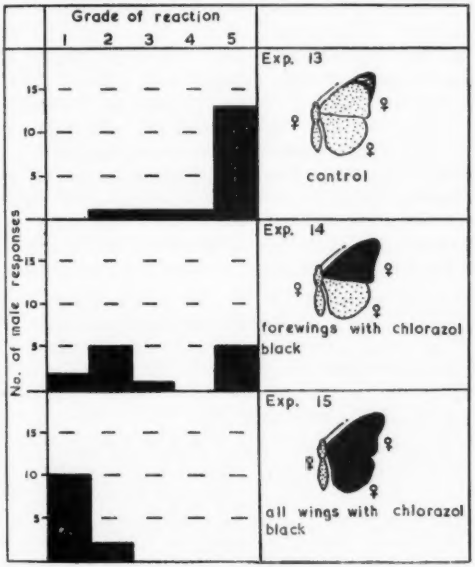

Fig. 7.

Certain of these visible properties were essential in promoting the earlier responses of the males.

*It is possible that the shape of the transparent, denuded, female wing was not appreciated by the males.

2. That the normal female wing possessed these properties and, in addition, certain other properties that encouraged the later responses of the male.

3. That these latter properties were not entirely absent from the test insect bearing the artificial wings, probably being present to a limited extent in the female body.

In order to distinguish the male responses due to the colour and brightness of the wings more clearly from those that were due to other factors (e.g., scent), the colour of a normal female test butterfly was painted out with a solution of chlorazol black in 50 per cent. alcohol. In this series of experiments (Fig. 7, Experiments 13, 14, and 15) the response of the males to a female test butterfly were determined successively after the following treatments:

1. The wings had been painted with 50 per cent. alcohol.

2. The forewings had been painted with chlorazol black.

3. The hindwings also had been painted with chlorazol black.

After each treatment the wings were allowed to dry before the tests were made. The attractive properties of the freshly killed female were not impaired by the alcohol (Experiment 13), and it is reasonable to attribute the changes in the male behaviour observed in the other two experiments to changes in the visible characters of the female wings. In experiment 14 nearly half the males gave a complete response indicating that the courtship sequence of the male did not depend on any pattern or colour that was peculiar to the forewing. The pattern of the female hindwing was extremely simple, consisting of an orange-brown ground with a narrow black border, but this pattern obviously provided sufficient stimuli to carry many of the males through the early stages of the courtship sequence during which visible stimuli were an important factor. The fundamental stimuli probably arose from the colour or brightness of the orange-brown scales. Since half the area of the forewing was occupied by a similar pigmentation it was thought that the greater frequency of complete responses occurring in experiment 13, as compared with experiment 14, was the direct result of the greater area of the orange-brown pigmentation that would have been visible to the males.

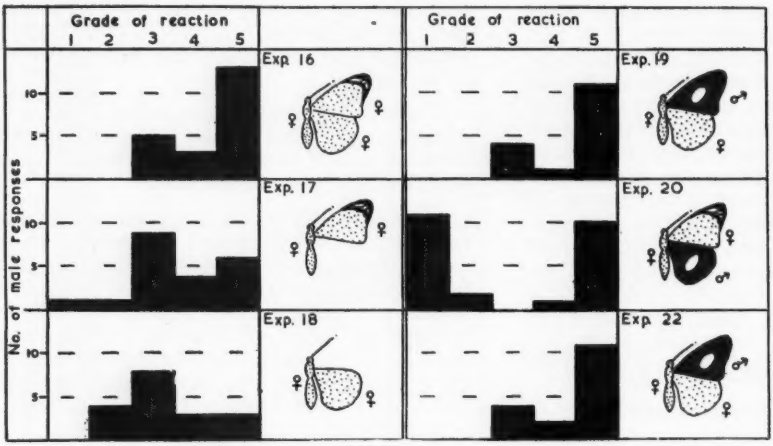

Fig 8.

(*d*) *The Significance of the Butterfly Shape, and the Dominant Effect of the Hindwings in producing the Male Responses.*

Some indication of the importance of these factors in eliciting the male responses may be obtained by a consideration of the results of experiments 16-22 (Fig. 8). Experiment 16 was merely a control experiment to confirm that the female to be used as a test insect was attractive to males. In experiment 17 this test insect possessed only its forewings, and in experiment 18 it possessed only its hindwings. In each case it appeared to be less effective in eliciting the responses of the males than it had been when both pairs of wings were present. When male forewings were added to the test insect used in experiment 18, thus producing a test insect with female body, female hindwings, and male forewings, the attractive properties of the insect were restored to a degree comparable with that of the complete female butterfly (Experiment 19). It was evident, therefore, that the addition of forewings to a test butterfly that possessed only the female body and hindwings markedly increased the responses of the males, and that this increase occurred irrespective of the sex of the added forewings. Since the shape and size of the added male forewings were approximately the same as in the female, although the wing patterns were quite different in the two sexes, it seems that the added forewing must have exerted its stimulatory effect by restoring a more "normal" shape or size to the test insect.

A very different result from that obtained in experiment 19, was obtained from experiment 20 for which the female bodyof the test insect was provided with female forewings and male hindwings, thus reversing the position of the wings with regard to their sex. A very marked "all or none" response was obtained from the males since they showed a very strong tendency either to give a very weak response or alternatively to carry the reaction sequence to completion (Experiment 20, Fig. 8). Out of a total of twenty-four responses there were, in fact, no Grade 3 response and only one Grade 4 response. This result could be explained on the assumption that the presence of the male hindwings not only reduced the attractiveness of the test insect, but also interpolated a positive block to further responses at an early stage in the courtship sequence. The only males to overcome this block may have been those in which the mating drive was rather strong, and they, having once overcome the block due to the male hindwings, were then able to carry the courtship sequence to completion.

In experiment 22 the sex of the wings was again reversed, so that the experiment was merely a repeat of experiment 19. The result was similar to that obtained in experiment 19, and there was no trace of the "all or none" reaction observed in experiment 20.

From the above experiments it was evident that the characters of the hindwing of the test insect were of great importance in releasing the courtship reactions of the males, and that they dominated the characters of the forewings. It was of further interest to determine whether the courtship sequence of the males was in any way adversely affected by stimuli arising from the male forewing, or whether it was entirely governed by stimuli arising from the hindwing. It had already been demonstrated (experiment 19) that if the test insect possessed

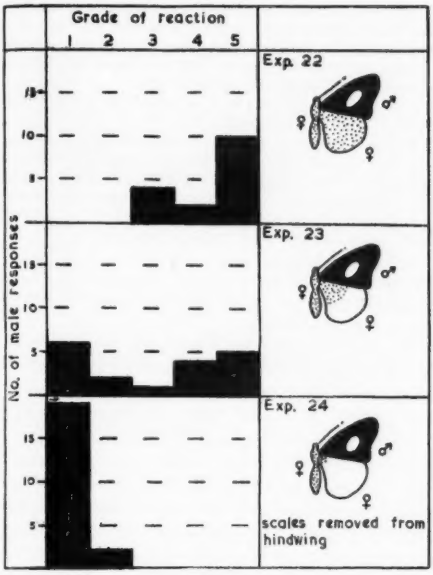

Fig. 9.

female hindwings it was more attractive to the males when it possessed male forewings than when it possessed no forewings at all. This observation, however, did not necessarily imply that no deterrent stimuli were arising from the male forewings, and further experiments showed that such stimuli were undoubtedly present (experiments 22, 23 and 24, Fig. 9). In order to demonstrate the presence of these stimuli the scales were progressively removed from the hindwings of the test insect used in experiment 22—this insect possessed male forewings and female hindwings. The removal of the scales presumably resulted in the progressive reduction in the intensity of the favourable stimuli arising from the female hindwing (see Fig. 6). If no adverse stimuli were arising from the male forewings it was to be expected that the progressive removal of the scales would result in a steady deterioration in the attractiveness of the test butterfly, and that this would be reflected in a steady decrease in the intensity of the male responses. If, however, adverse stimuli were arising from the male forewings a somewhat different result was to be expected. Under these circumstances there would come a time during the progressive reduction of the favourable stimuli from the female hindwings when these stimuli would be approximately balanced by the adverse stimuli of the male forewings. The adverse male stimuli would then tend to "block" the reaction sequences of some of the living males at an early stage in the response (see experiments 2a, 3, 6, 9, etc.), and thus give rise to an "all or none" response similar to that seen in experiment 20. Experimentally such an "all or none" response was found to occur when the scales had been removed from the distal half of the hindwing (experiment 23). This indicated that certain features of the male forewing tended to inhibit the courtship behaviour of other living males. In experiment 22, however, any inhibition or other effect arising from the male forewings of the test insect were obscured by the predominant effects of the hindwings.

(*e*) *Experiments on the Inhibitory Effects of the Male Test Butterfly during the Later Stages of the Courtship Sequence.*

The experiments already described had indicated that certain characters of the male butterfly were able to inhibit the courtship sequence in other males, and that this inhibition occurred during the early stages of the sequence. It was uncertain, however, whether the male characters could exert a similar inhibition during the later stages of the sequence. In order to investigate this matter the courtship sequence was induced in living males by means of a female test insect, and attempts were then made to substitute a male test insect during the later stages of the courtship responses. The males always followed the test female very closely, and it was not possible to effect a satisfactory substitution at any stage of the courtship sequence earlier than the Grade 4 reaction. Even males that had settled on the ground beside the test insect (i.e., Grade 4 reaction) remained alert and ready to follow any movement of the test insect, so that it was often difficult to effect the substitution. The following observations were recorded on individual males.

Experiment with Living Male A

It was, at first, extremely difficult to substitute the male test insect since the male A followed the female test insect very closely. Eventually, however, the male was decoyed into some rather coarse grass by means of the female test insect. This grass somewhat impeded the flight of the male, and prevented it from making an *immediate* pursuit after the female test insect when the latter was moved away. In the short delay that occurred before the male would take flight it was possible to remove the female test insect, and substitute a male test insect by placing the latter beside the living male. The latter then readily accepted the male test insect. This procedure was successfully repeated twice more. On each occasion the living male butterfly treated the

male test insect as though it were a female, crawling over and around it with fluttering wings, and attempting to copulate with it. On each occasion also a loose union was formed between the genitalia of the two insects.

When the test insect was moved slowly away the living male followed it closely. If the test insect was moved more rapidly so that a greater distance (perhaps about a foot) lay between the insects, the living male seemed suddenly to appreciate the "maleness" of the test insect and then showed no further interest in it. The sequence of reactions had been broken, and could only be initiated again by means of the female test insect.

Finally, by substituting the male insect as before and then moving it to stroke the living male butterfly a state of catalepsis was induced in the latter insect (grade 5 response).

Experiment with Living Male B

This male showed little interest in the female test insect, a grade 2 response being the strongest response that it was possible to obtain.

Experiment with Living Male C

As with male A a certain amount of difficulty was experienced in the substitution of the male test insect, but it was overcome by the same ruse of enticing the butterfly into coarse grass. Substitution was effected three times, and each time the living male butterfly reacted as though the male test insect were a female, and attempted to copulate with it.

Finally, a state of catalepsis was induced in the male by means of the female test insect. The male was then transferred to the cork supporting the male test insect and "awakened" by gently tapping its wings. On thus becoming active again, male C immediately tried to copulate with the male test insect.

Experiment with Male D

This male followed the female test insect very closely, and since it was inhabiting an open stony area with very little vegetation, substitution of the male test insect was not possible.

Experiment with Males E and F

Males E and F were attracted to the female test insect simultaneously, and both settled on the ground beside it (Grade 4 response). The test insect was then quickly removed, but on this occasion neither male attempted to follow it. Instead they remained together for nearly a minute, fluttering around each other in an agitated fashion, and gradually moving across the grass to a point some 3 to 4 feet away from the place where they had originally settled beside the test insect. They then separated and flew away.

Since two males were involved in the above observation, and since both behaved in a similar fashion, it is reasonable to suppose that the behaviour observed would not have been uncommon had a greater number of similar observations been made, and some significance may be attached to the observation. The outstanding feature of the behaviour of the two males was the complete absence of the "aggressive" behaviour that was usually seen when two males came into close contact. It was not unusual for a male that was showing a Grade 4 response to a female test insect, to carry out a brief fluttering search of the area if it failed to follow the test insect when the latter was suddenly removed. This behavioural tendency may have been one factor contributing to the observed behaviour of males E and F, but it seemed significant that they remained in association even after they had moved away from the place originally occupied by the test insect. There was thus not only an absence of the "aggressive" factors normally observed in the behaviour of males towards each other, but also some evidence that the males were attracted to each other.

After the observation on the joint behaviour of males E and F had been completed, a female test insect was presented to male E. As in the previous experiments a male test insect was substituted when the male had attained a Grade 4 response in the courtship sequence. The male accepted the male test insect, continually crawled over it, and was obviously attracted to it strongly. No attempt, however, was made to copulate.

Experiment with Male G

Although the male test insect was successfully substituted the male was not attracted to it, and flew away.

Experiment with Male H

This male followed the female test insect so closely that it was not possible to substitute the male test insect.

The observations made during this series of experiments indicated that the stimuli necessary to elicit the *final* stages of the courtship sequence from the male were provided equally well by male and female test insects. If scent should prove to be a dominant factor in these responses then the scent concerned will presumably be found to be associated with the species rather than with either particular sex. It was also evident that if the male test insect were moved more than a certain distance (perhaps some 12-18 inches) from a living male that was showing a Grade 4 response to it, then the living male appeared to appreciate the "maleness" of the test insect and made no further courtship responses.

(*f*) *Experiments on the Reactions of Male H. misippus to Female D. chrysippus Test Insects.*

The reactions of the male *H. misippus* to *D. chrysippus* were investigated because of the mimetic resemblance existing between the females of the two species. The primary object was to determine at which stage in the courtship sequence the male *Hypolimnas* was able to distinguish its own females from those of the danaids. Throughout the investigation only one varietal form of each butterfly was used. This was the *alcippus* form of the danaid, it being the only one available at Achimota, and the typical female form of *H. misippus*.

In experiment 25 (Fig. 10) a freshly killed danaid female was used as the test insect. It proved quite unattractive to the *Hypolimnas* males, the majority of which merely inspected it from a distance of some 6 to 24 inches and then flew away. Clearly the *Danaus* female possessed

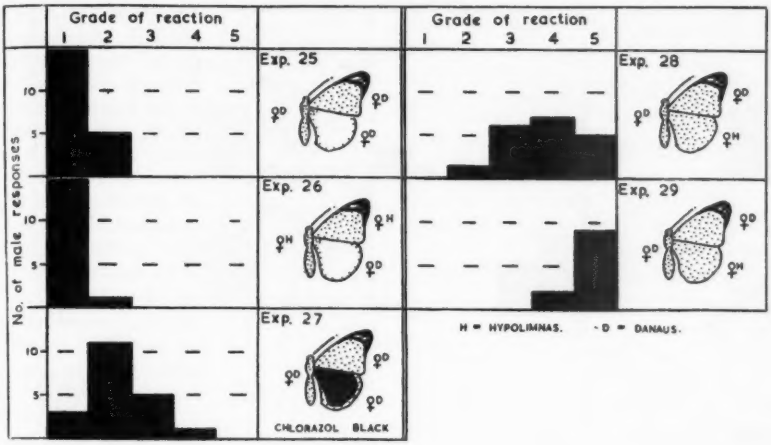

Fig. 10.

a certain feature or features which tended to inhibit the courtship sequence of the *Hypolimnas* male in its earliest stages. The factor or factors involved were presumably of a visual nature since they were perceived by the *Hypolimnas* males from a distance.

It has already been stated that the *alcippus* form of *D. chrysippus* is characterised by the white ground colour of the hindwing, and that this was the only form found at Achimota. On the other hand the white-hindwinged forms of *H. misippus* were absent from Achimota, so that the presence or absence of the white hindwing constituted a constant and conspicuous difference between the two species in this area. The earlier experiments had shown that the characters of the hindwing of the test insect exerted a dominant influence over the stimulation or inhibition of the courtship sequence of the male *Hypolimnas*. The white colouration of the danaid hindwing was, therefore, not only a conspicuous pigmentary difference between the two species, but it was also situated on that part of the butterfly which tended to dominate the courtship reactions of the male *Hypolimnas*. It seemed probable, therefore, that this white hindwing would prove to be an important factor in the inhibition of the *Hypolimnas* courtship behaviour that had been observed in experiment 25. The following experiments gave a considerable support to this view.

That the inhibition of the courtship sequence arose from the danaid hindwings was demonstrated in experiment 26 (Fig. 10). In this experiment the hindwings of a female *Hypolimnas* test insect, previously shown to be attractive to males, were replaced by the hindwings of a female danaid. The resulting test insect, which possessed the body and forewings of the *Hypolimnas*, and the hindwings of the danaid, was no longer attractive to the males.

The results of experiment 27 (Fig. 10) indicated that this loss of the ability of the test insect to elicit the courtship behaviour in the *Hypolimnas* males was due, at least in part, to inhibitory stimuli arising from the white pigmentation of the danaid hindwing. For this experiment the female danaid test insect from experiment 25 was again used, but on this occasion the hindwings were painted over with an alcoholic solution of chlorazol black, thus obliterating the white pigmentation. It will be seen from Fig. 10 that there was a marked increase in the response of the *Hypolimnas* males to the danaid test insect as a result of this treatment, although none of the naturally occurring varieties of the *Hypolimnas* female possess black hindwings.

For experiment 28 (Fig. 10) the blackened hindwings of the test insect used in experiment 27 were replaced by the hindwings of a freshly killed *Hypolimnas* female. The test insect thus possessed the body and forewings of the danaid female, but combined with the hindwings of the *Hypolimnas* female. The presence of the *Hypolimnas* hindwings greatly increased the responses of the *Hypolimnas* males, even though the experiment was performed rather late in the afternoon when the males were becoming less active. Two days later the experiment was repeated with the identical test insect, but during the morning (Experiment 29, Fig. 10). On this occasion the response of the males was very strong, most of them responding with the complete courtship sequence of behaviour.

The experiments described in this section emphasised once again the dominant effects of

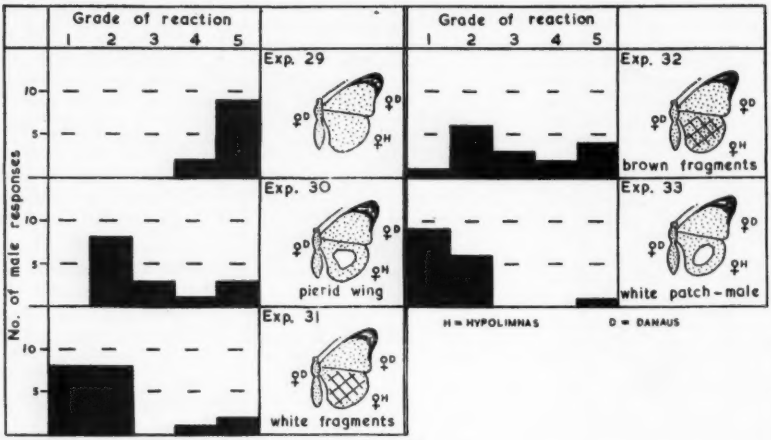

Fig. 11

the hindwings of the test insect on the responses of the males. They also suggested that a white area on the hindwing might exercise a strong restraint on the male courtship behaviour.

(*g*) *The Inhibition of the Courtship Behaviour of the Hypolimnas Male by a White Area on the Hindwing of the Test Insect.*

Further experiments were devised to investigate the deterrent effects of white hindwings on the courtship behaviour of the male *Hypolimnas*, for the existence of such a phenomenon was of considerable biological interest. Not only did it provide an explanation for the absence of the white-hindwinged forms of *H. misippus*, but it also indicated a sexual selection operating *against* the development of a closer mimetic resemblance of *H. misippus* to *D. chrysippus* in this part of Africa (see later).

In making the desired experimental alterations to the pigmentation of the wings there was always the possibility that the normal olfactory stimuli might be disturbed, either by the addition of a repellent odour or by the removal of an attractive one. For this reason the coloration was changed either by the addition of fragments of butterfly wings or by the use of Rowney's powder paints. It seemed unlikely that either of these would possess a repellent odour, especially if the fragments of butterfly wings were taken from other specimens of *H. misippus*.

In experiment 30 (Fig. 11), a small circle of cream-coloured wing was cut out of a pierid wing and stuck to the hindwing of the test insect used in experiment 29. The circle of pierid wing covered rather more than half of the brown area of the *Hypolimnas* hindwing, and it will be seen from Fig. 11 that its presence caused a considerable reduction in the strength of the responses made by the *Hypolimnas* males. This reduction may not have resulted entirely from visual stimuli, however, as it was possible that the pierid wing possessed some odour that was repellent to the *Hypolimnas* males.

In order to overcome this criticism the same test insect was next provided with wings taken from an attractive *Hypolimnas* female, but in which the greater part of the brown area had been obscured by fragments of white wing obtained from the forewings of *Hypolimnas* females (Experiment 31, Fig. 11). These small fragments of wing gave the hindwing of the test insect a rather rough appearance which might in itself have discouraged the males. A control experiment was therefore necessary in which the hindwings of the test insect were covered with small fragments of brown wing also taken from the forewings of female *Hypolimnas* butterflies (Experiment 32, Fig. 11). In comparing the results obtained in experiments 29, 31, and 32, it will be seen that the test insect elicited a considerably weaker response when the hindwing was covered with fragments of brown forewing (Experiment 32) than when it was in its original state (Experiment 29). Since the colour of the hindwing was apparently unaltered by the addition of the fragments of brown wing it seemed likely that the weaker responses were the result of the rough appearance of the wing. An even weaker response, however, was obtained when the hindwing was covered with fragments of white wing, and it seems reasonable to attribute this further fall in the male responses (Experiment 31) to the inhibitory effect of the white pigmentation placed on the hindwings.

Further evidence of the inhibition was obtained in experiment 33 (Fig. 11). In this a female

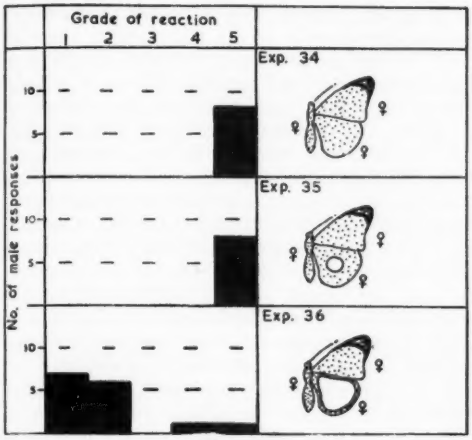

Fig. 12.

Hypolimnas test insect was used, but the hindwings each carried a large white patch obtained from the forewings of a male *Hypolimnas*. Considerable evidence had already been acquired indicating that the male wings carried no scent that was repellent to living males (e.g. the substitution experiments with the living males A to H already described in this paper), and the failure of the test insect to attract the males in this experiment may be fairly attributed to the presence of the white patch on the hindwing.

Some idea of the size of the white area necessary to inhibit the responses of the males was obtained from experiments 34, 35, and 36 (Fig. 12). In experiment 34 the test insect was a female *Hypolimnas*. In experiment 35 a circle of Rowney's powder paint was applied to the centre of each hindwing of the same test insect, each circle having a diameter of approximately 1 cm. It will be seen that the responses of the males were not appreciably reduced by this treatment. When, however, the white areas were extended almost to the margin of the wings thus reproducing the condition found in *D. chrysippus*, form *alcippus*, the courtship responses of the males were almost completely inhibited (experiment 36).

Discussion

(*a*) *The Validity of the Comparisons made between Separate Experiments.*

It will be evident that the conclusions to be derived from the experimental work are obtained in the main, by a comparison of the results obtained in various experiments. The validity of such comparisons must therefore be examined.

Taking the entire series of experiments as a whole it seems likely that three factors would be of particular significance in any comparison that might be made between any individual experiments. They are as follows:

(i) Unrecognised differences between apparently similar test insects.

(ii) Differences in the excitatory state or sensitivity of the *Hypolimnas* males to which the test insects were offered.

(iii) Changes in the skill of the experimenter in eliciting a high grade response from the butterflies.

In order to reduce the possibility of serious errors arising from the operation of the first factor, the attractiveness of each female *Hypolimnas* was confirmed before it was utilised in any of the experimental work. It was, in fact, never necessary to discard any female on the grounds of unattractiveness during the experimental work here described, but the discovery of an unattractive female during the preliminary trials indicated the necessity of making the confirmatory tests. It is unlikely that any serious errors entered the experimental work from this source.

The second possible source of error (i.e. variations in the sensitivity of the living males was much more serious, the general level of the sensitivity of the males being much affected by the climatic conditions and by the time of the day. The effect of this factor on the experimental results may be seen in the response of the males to the test insects C and D in experiment 1 (Fig. 3). The responses were much less complete on the second day than they had been on the first, and this was almost certainly due to the more unfavourable conditions on the second day, later experiments indicating that the attractiveness of the test insect was unlikely to have shown any significant decrease over such a short period of time. Throughout the second day, in fact, the sun was almost continuously obscured by heavy clouds, and the tests had to be made during the few short periods of sunshine that did occur. In the absence of the sunshine the *Hypolimnas* males were inactive, and when they did fly it seemed that they were much less sensitive than usual to the presence of the female test insects. However, such considerations do not invalidate the comparison made between the responses obtained to A and

B, and those obtained to C and D on the same day, since these tests were carried out under approximately the same conditions. For this reason the experiments of the investigation were carried out in short series, each series normally comprising only 3 or 4 separate experiments. Such a series could be completed within a reasonable period of time (2 to 24 hours). In view of the results obtained in experiment 1 no further experimental work was carried out on excessively cloudy days.

The third source of error suggested above concerned a possible increase in the skill of the experimenter in eliciting high grade responses from the males. Even when using a standard method of presentation of the test insect, it would have been most surprising if the presentation had not "improved" with practice. Here again, however, the use of small series of experiments, completed on one day, presumably reduced the effects of this type of error.

(*b*) *The Role of Sight in the Courtship Sequence of the Male.*

There can be no doubt that, as in many other diurnal insects, the earlier stages of the courtship sequence of *H. misippus* are dominated by the sense of sight. This was indicated by the extreme readiness with which the males arose to investigate other flying insects or birds, even though the latter were some distance away.

Although the significance of the butterfly shape and size was not investigated, there was some evidence (experiments 18, 19) that quite moderate changes in one of these factors at least was able to influence the behaviour of the males. Even if it is accepted that the test insect of experiment 19 was more attractive than that of experiment 18, it is not possible to separate the effects of the shape from those of the size, since both were restored to normal by the addition of the male forewing. Any effect of colour or brightness as a beneficial factor in this experiment may be discounted, later experiments (22, 23, 24) showing that the visual stimuli from the male forewing had a repellent effect on living males.

It is quite evident that the male reactions were decided predominantly by the sex of the wings of the test insects, the sex of the body having only minor significance. Only low grade responses were obtained when the test insect possessed male wings. For the following reasons it seems that the wings exerted their dominant influence on the early stages of the courtship sequence as a result of visual rather than odoriferous stimuli.

1. The substitution experiments in which a male test insect was substituted for a female one during the final stages of the sequence suggested that the male possessed no scent that acted as a sexual repellent to other males.

2. The responses of the males decreased when the female colouration of the test insect was blackened over in a fashion unlikely to affect any odoriferous stimuli arising from them (Fig. 7).

3. A test insect elicited stronger early responses when it possessed painted paper wings than when it possessed female wings from which the scales had been removed.

4. A danaid female was also found to be relatively attractive during the early stages of the sequence provided that the white area on the hindwing had been blackened (Fig. 10). The danaid would not, presumably, possess the same specific smell as a *Hypolimnas* female.

5. The males generally failed to inspect a white test insect (e.g. *Pieris calypso*), even when presented so that it must have been clearly visible to them. It seemed that the white colouration or the brightness of the test insect almost completely inhibited the male reactions.

(*c*) *The Dominant Effect of the Hindwing of the Test Insect in determining the Responses of the Male Butterflies.*

The first indication that the forewings and hindwings of a complete test insect did not exert an equal effect on the male courtship sequence was noticed in experiments 16, 20, and 21. In these experiments the substitution of male forewings in an otherwise female test insect did not reduce the responses of the males. When the substitution was made in the hindwings, however, the reactions of many males were inhibited, thus giving rise to the "all or none" response in Fig. 20.

(*d*) *The Response of the Male Hypolimnas to D. chrysippus.*

The *Hypolimnas* males gave only a low grade response to *D. chrysippus* test insects (form *alcippus*). An examination of the experiments of Figs. 10 and 11 leaves little doubt that this was due largely to the presence of the white hindwing. There was, for instance, a marked increase in the responses of the males when the white area of the danaid hindwing was obliterated with chlorazol black. It would seem that

the white hindwing blocked the reaction sequence in the early visual stages, and that the chlorazol black had removed this block. Even so, it was not to be expected that the reactions would go to completion, since the specific *Hypolimnas* scent, presumably necessary for completion, would be absent from the danaid. Experiment 27, in fact, probably represented the response of the males to visual and behavioural stimuli only. It was probably a suboptimal response to such stimuli since the hindwings were black, not the more attractive brown of the *Hypolimnas* female.

When the hindwings of the danaid test insect were replaced by those of a female *Hypolimnas*, the resulting test insect was highly attractive to the males (Experiment 29). This attractiveness was reduced again, however, when white patches were fastened to the hindwing, even though the patches had themselves been taken from the wings of *Hypolimnas*. There was considerable evidence (expts. 29-33) that the repellent effect of these white patches was largely due either to their brightness or white pigmentation.

In view of the previous findings these results are not surprising, for the white area of the danaid was large, and this alone would have tended to inhibit the male responses. In addition. however, it was sited on those parts of the test insect which were known to dominate the responses of the males, namely the hindwings. The white hindwings of *D. chrysippus* form *alcippus*, therefore, effectively blocks the courtship reactions of the male *Hypolimnas*.

(*e*) *On the Mimetic Association between H. misippus and D. chrysippus.*

The mimetic association between *H. misippus* and *D. chrysippus* has often been quoted in the literature as a classical example of butterfly mimetism (e.g. Eltringham, 1910; Punnett, 1915; Grassé, 1951). The association attracted attention owing to the abundance and wide distribution of the species concerned, the marked departure of the female *Hypolimnas* wing pattern from the type found in other members of the genus, and the existence of the parallel female forms illustrated in Fig. 1. Although it is reasonable to suppose that the similarity in the wing patterns of the two species had its origin in a mimetic selection, it does not follow that such a selection operates wherever the two species exist together. At the present time the significance of the mimetism is somewhat obscured by the fact that the geographical distributions of the various female forms of *H. misippus* do not correspond with those of the equivalent forms of *D. chrysippus* (Eltringham, 1910). This was well illustrated at Achimota where no forms of *H. misippus* with white hindwings were seen, and yet the *D. chrysippus* population consisted entirely of the form *alcippus* which has conspicuous white hindwings. Furthermore, the behaviour of the *Hypolimnas* males at Achimota indicated that there would be a strong sexual selection against any females that happened to possess white hindwings (e.g. Fig. 12). Although many *Hypolimnas* females taken at Achimota had a gentle suffusion of white scales on the hindwings, the effect of the scales was slight, and they did not destroy the general brown colouration of the wings. It seemed, therefore, that the ability to develop a white hindwing was genetically inherent in the *Hypolimnas* female, but that the evolution of the form *alcippoides* (with white hindwings) was prevented by the courtship selection of the males. Had a mimetic selection been operating in the Achimota district, it would, presumably, have selected against this male tendency to avoid females with white hindwings, as other factors being equal, the progeny of a male willing to mate with a mimetic female (i.e. white winged) would presumably stand a greater chance of survival than those of a male that would mate only with non-mimetic (brown-winged) females. It was, therefore, concluded that no mimetic selection was operating on *H. misippus* females in Gold Coast or the other West African areas where the *alcippus* form of *D. chrysippus* predominates.

The statements in the literature, noted above, suggesting that *H. misippus* form *alcippoides* was a mimetic form corresponding to *D. chrysippus* form *alcippus*, implied that in some areas, at least, the former butterfly would be relatively frequent. This was of interest in the present connection since the males in such areas could hardly have a strong aversion to females with a white hindwing. An enquiry to the Department of Entomology, The British Museum (Nat. Hist.), regarding the distribution of *H. misippus* form *alcippoides*, was kindly answered by Mr. A. G. Gabriel. He stated that this form appeared to be "very uncommon" throughout the extensive range of the species, and that of the large number of specimens of the species in the Museum collections, only two belonged to this form.

In view of the scarcity of *H. misippus* form *alcippoides*, the present author feels that it should be regarded, not as a mimic of *D. chrysippus* form *alcippus*, but rather as a rare mutation of the *Hypolimnas* which happens to resemble the *alcippus* form of the danaid. If this view is accepted it follows that there is no truly mimetic form of the *Hypolimnas* corresponding to *D. chrysippus* form *alcippus*. The frequent occurrence of females with a white suffusion on the hindwings suggests, however, that the failure of the *Hypolimnas* to develop such a form is not due to any genetic inability to do so. Presumably, therefore, the *Hypolimnas* can derive no biological advantage by the development of such a form, i.e., no mimetic association exists between the two species of butterflies in those areas where *alcippus* is the dominant form of *D. chrysippus*.

Summary

1. The male of *H. misippus* responds to the female with a characteristic sequence of courtship reactions.

2. Test insects were prepared from the wings of freshly killed butterflies. They were presented to free-living males in a manner that allowed the males to respond to them with the courtship sequence of reactions.

3. The early stages of the courtship sequence were under the control of visual stimuli, but the later stages were controlled by other stimuli, probably of a behavioural and chemosensory nature. These latter stimuli were present in both male and female test insects, and were, therefore of specific rather than sexual nature.

4. Stimuli arising from the wings of a male test insect had an inhibitory effect on the courtship reactions of living males.

5. Stimuli arising from the hindwings of a test insect had a more pronounced effect on the behaviour of the male than similar stimuli arising from the forewings.

6. The courtship sequence was strongly inhibited in its early stages by white or light coloured test insects.

7. The presence of white hindwings on the test insect exerted a strong inhibitory effect on the courtship reactions of the male. For this reason the male *Hypolimnas* was not normally attracted to *D. chrysippus* form *alcippus*. The latter resembles closely one of the female forms of *H. misippus* but possesses white hindwings.

8. It is suggested that there is no mimetic form of *H. misippus* corresponding to the *alcippus* form of *D. chrysippus*. The female form *alcippoides* of *H. misippus* is too scarce to be regarded as a true mimetic form.

9. It is further suggested that, since *H. misippus* appears to be genetically capable of developing the *alcippoides* form, no true mimetic association exists between *H. misippus* and *D. chrysippus* in those areas where the form *alcippus* of the latter species is dominant.

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CHANGES IN NEST BUILDING BEHAVIOUR IN MULTIPAROUS RABBITS

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The purpose of this paper is to present data concerning systematic changes in the quality of nests built by multiparous rabbits. A recent conference on parental age and characteristics of the offspring has called attention to some significant effects of parental age and to some litter seriation effects (Miner, 1954). Behavioural aspects, however, were not discussed widely, and there is not much evidence in the literature to indicate that there are any significant developmental aspects of nest building behaviour.

Wiesner & Sheard (1933) report no consistent differences in the mode of parturition of primiparous and multiparous female rats. Beach (1937) studied the effects of cortical lesions on the maternal behaviour pattern in the rat. He found that primiparous rats which had been reared in individual cages up to the time of parturition, cleaned and cared for their young and fixed nests in a biologically adequate fashion, even though they had never seen nests built or delivered litters. Munn (1950) reviewed the literature dealing with maternal behaviour in the rat. He describes the behaviours involved and some of the neural and endocrine factors underlying these behaviour patterns, but does not report upon developmental changes as a function of number of litters.

Recently Sawin & Curran (1952) and Sawin & Crary (1953) have reported on a large scale investigation of maternal and reproductive behaviour in the rabbit. These workers obtained results clearly indicating that genetic differences exist in nest building characteristics. These differences have been related to pituitary and sex hormone balance. An hypothesis was advanced that "time of nesting and the nature of the nest and lining are determined by the existing balance of pituitary and ovarian hormones, the first being triggered by the increasing level of prolactin, and the stronger manifestation of the latter being determined by the duration of optimal balance of the ovarian hormone" (Sawin & Crary, 1953, p. 144). This hypothesis certainly does not necessarily imply that developmental changes are to be suspected, unless one wishes to assume certain systematic changes in hormonal level with each succeeding litter.

Even though little in the way of developmental changes in nest building have been found, there is clear evidence that environmental manipulations can modify maternal behaviour. Wiesner & Sheard (1953, p. viii) report that ". . . we may claim to have demonstrated . . . that maternal behaviour can arise, and can be evolved artificially, in the complete absence of the somatic conditions which are usually and normally associated with maternity." Riess (1954) reported that female rats, reared in cages with no objects which could be picked up or transported, do not build nests at parturition, even though the appropriate material is provided at that time. Riess also cites the work of Birch in which female rats were reared with rubber collars around their necks. These collars prevented the female from washing herself and from mouth contact with her genitalia. The collars were removed before parturition, and it is reported that these experimental females failed to clean or nurse their young. These studies have methodological and theoretical importance in the analysis of what has been called instinctive behaviour. Since there is evidence that experience does play some role in the maternal behaviour of primiparous female rats, we have asked a question about nest building performance in the rabbit. Our question has not been about the determinants of the first nest constructed by primiparous female rabbits, but rather about the quality of nest construction and its changes with repeated parturitions. We have been fortunate in having available the data of some five years of intensive study by Sawin and his collaborators for the analysis. Our hypothesis is that the quality of nest construction will improve with successive parturitions.

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Method

Nest Building Process

The animals of this colony are housed in outdoor hutches. The breeding does are housed in cages approximately 7 ft. square. Two days before parturition, each mother is provided with a nest box which measures 23″ × 11″ × 11″ on the inside. The box contains a 6″ high partition which divides the box into two compartments and a removable lid covering two-thirds of the box. The floor of the rear compartment of the box is covered with a ½″ thick layer of shredded sugar cane which serves to absorb excess moisture in the box. This compartment is approximately three-quarters filled with loose excelsior. A lid is fitted to the box, and the box is then placed in the rabbit's pen. Figure 1*a* shows an unprepared nest box, and 1*b* shows a box ready for use.

Sawin & Crary (1953) have observed that in preparation for nest construction, the rabbit usually begins actively to collect in her mouth, straw, hay, excelsior, or other similar available material. These materials are deposited in the location selected for the nest. When sufficient quantities of nesting material are accumulated, she burrows into it, and usually makes a hollow. After the nest is constructed, or even before, the mother normally plucks hair from her body which is finally used to line and cover the nest. The degree to which it is hollowed, arranged and covered characterises the nature of the nest. Figure 2 shows photographs of poor, fair, good, and excellent nests.

Rating of Nest Quality

The observations on which this analysis is based were made the day the litter was born usually between 8 a.m. and 9 a.m. Various observations on maternal behaviour and lactation were made, including such characteristics as location of nest, time of nest building, quality of nest, quantity of nest lining, scattering of young, cannibalism, lactation, etc.

The scale from which the nest quality scores is derived is based on the degree to which the nest is hollowed out, arranged, and covered. Sawin & Crary (1953) report that some mothers, after constructing a nest and bearing the young, will cover the nest with additional nesting material. often filling the box almost completely. Thus, the "packed" is considered the best, since it gives additional protection and conservation of heat. It should be noted that measures of ambient temperature were recorded, and that litters in our analysis occur over the entire year. Figure 3 illustrates graded classes of nests produced by the rabbit according to Sawin & Crary (1953). Number O illustrates the case in which no apparent effort at all was made to build a nest. Number 6 illustrates a well-hollowed packed nest.

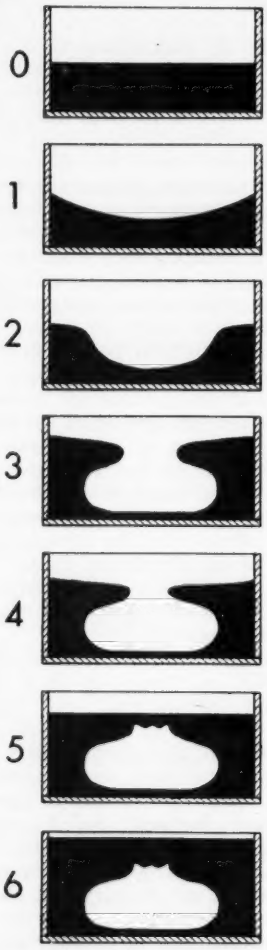
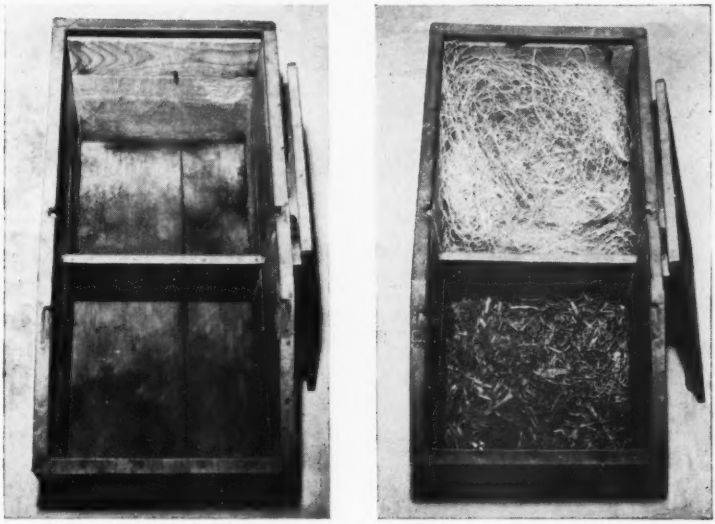


Fig. 3. A schematic drawing of the graded classes of nests.

The observations were made by Sawin and three assistants each as carefully trained as possible in making the ratings. Because of the

PLATE I



(*a*) (*b*)

Fig. 1. (*a*) An unprepared nest box.
(*b*) A nest box ready for use.

PLATE II

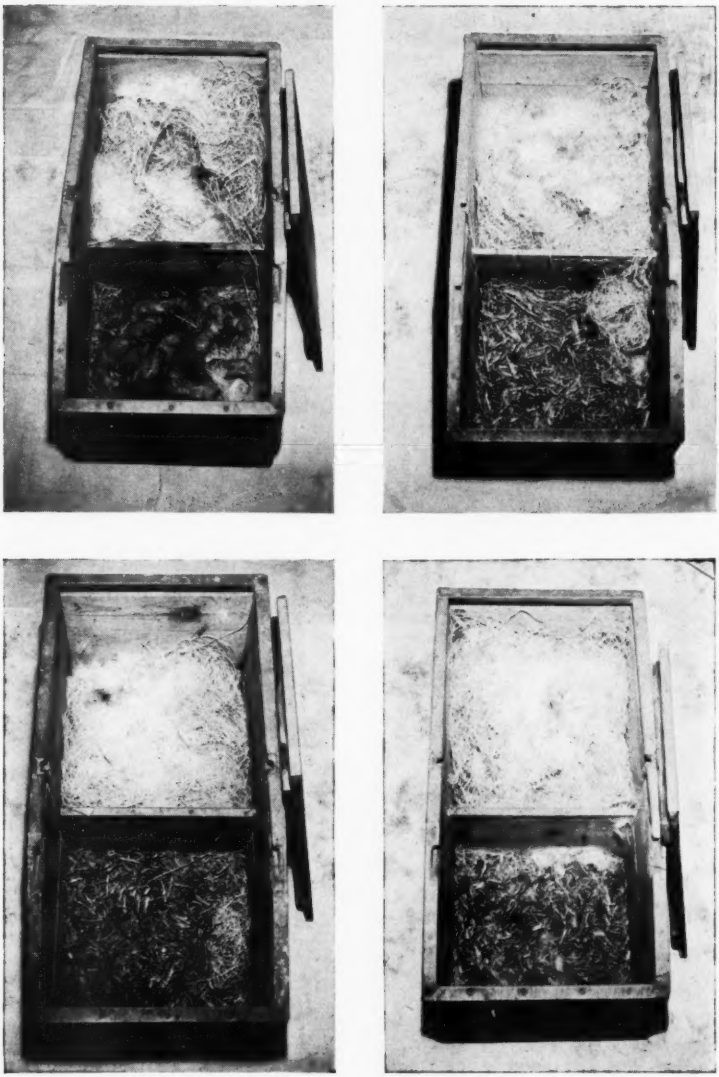


Fig. 2. Nests of varying quality.

Upper left. Nesting material shows no hollowing. Hair is scattered and tramped and young are scattered in front of box.

Upper right. Nesting material is considerably compacted with a minimum of hollowing and hair somewhat scattered.

Lower left. Nesting material is fluffed and considerably hollowed. Hair is concentrated within the hollow and around the opening.

Lower right. Nest is well hollowed and lined with hair, with a small aperture through which the thickly concentrated hair is protruding. Nesting material is loose and fluffed.

Table I. Showing N, Mean and S.D. of the Nest Building Rating for Four Litters for Each Race and Subline

Race	N	Litter 1		2		3		4	
		Mean	S.D.	Mean	S.D.	Mean	S.D.	Mean	S.D.
X	21	2·14	·985	2·62	·785	2·48	·794	2·38	·999
III	14	2·07	·810	2·43	·823	2·50	·626	2·64	·895
IIIc	20	1·70	1·45	1·85	1·11	2·30	·955	1·95	1·06
IIIr²	7	2·29	·880	2·57	1·05	2·71	1·16	2·42	·730
AcEp	22	2·50	1·16	2·50	·865	3·00	·742	3·00	·855

extended period of time involved, the large total number of animals (800) at all ages and in different races, and the number of characteristics being recorded at the same time, there seems little likelihood of any systematic bias towards any part of the scale in successive parturitions.

Subjects

The analysis is based on results from three partially inbred races of rabbits, designated as race X, race III, and race AcEp. Two other groups of rabbits, designated IIIc, and IIIr², which are sublines of race III, were also used.

The mean age of the mother rabbit at the time of the first litter is approximately 6-7 months. The usual weaning period for rabbits is 2 months. If the mother fails in lactation, the young may be fostered by another available lactating rabbit. A litter of young rabbits of 4 or more is usually shifted to a pen twice the size at one month of age. Otherwise, it usually remains in the same pen until the age of four to five months. At this time the bucks are removed, placed in separate pens, while the does often remain together even after they have been mated and are near parturition. All are separated, however, at least 3 days prior to expected parturition.

The available data from the hundreds of rabbits were inspected with the objectives of selecting rabbits which had borne several litters, and of maintaining minimally adequate numbers of subjects for meaningful statistical analyses. This inspection showed that as the number of litters increased, the number of rabbits who had these litters decreased rapidly. Since the major criterion was number of litters we decided to sacrifice the vast majority of our population and choose all mothers which had had exactly four litters. This elimination left 7 to 22 mothers in the various races.

Results and Discussion

Table I shows the characteristics (N, M, SD) of the nest building ratings for each of the races

Table II. Analysis of Variance of Nest Building Rating for three Race III Strains

Source	*df*	*SS*	*MS*	*F*	*P*
Strains	2	10·00	5·00	3·11	·10
Subjects within strains	38	61·11	1·61		
Litters	(3)	(5·63)			
Linear	1	3·43	3·43	4·08	·05
Quadratic	1	1·76	1·76	2·10	N.S.*
Cubic	1	·44	·44	—	N.S.
Strains x Litters	6	1·46	·24	—	N.S.
Subjects x Litters	114	96·16	·84		
Total	163				

*Not significant

Table III. Analysis of Variance of Nest Building Rating for Races AcEp and X

*Source**	*df*	*SS*	*MS*	*F*	*P*
Litters	(3)	(4·56)			
Linear	1	3·65	3·65	4·74	·05
Quadratic	1	·84	·84	1·09	N.S.
Cubic	1	·07	·07	—	N.S.
Races x Litters	3	3·47	1·16	1·51	N.S.
Subjects x Litters	123	94·48	·77		

*The complete analysis is not included here. Only that portion concerned with the analysis of the functional relationship of the litter effects is presented. See Table IV for a complete analysis of these two races plus race III.

and sublines. The first analysis was of the three related strains of race III in which an analysis of variance was performed to test for subline differences and for a functional relationship among the litter means (Snedecor, 1946; Denenberg, 1954). The analysis is shown in Table II.

A significant linear relationship between rated quality of nest and litters was found, and the quadratic and cubic effects were both insignificant. Our interpretation is that the quality of nest built by these rabbits improved significantly in a linear fashion from the first to the fourth litter. The lack of a significant interaction effect for strains x litters means that this generalisation can be made for all three sublines in race III. In addition to this analysis the test for differences among the strains is significant at the 10 per cent. level.

To check on the validity of the finding of a linear function, races AcEp and X were analysed in the same manner as described above to see if a significant linear function was also found here. The results are presented in Table III.

It can be seen that the linear component is significant at the 5 per cent. level. Again, neither the quadratic nor the cubic components approach significance.

These two independent analyses substantiated the hypothesis that there is a significant linear improvement in the quality of nest built for each succeeding litter, and that this change holds for all five races.

A third analysis was made using races X, AcEp, and III. This analysis is presented in Table IV. Here the linear component is significant at the 1 per cent. level and the differences among the races is significant at the 5 per cent. level. In addition the interaction between races and litters is insignificant, permitting a generalisation to all races and groups in the populations studied.

Table IV. Analysis of Variance of Nest Building Rating for Races III, X and AcEp

Source	*df*	*SS*	*MS*	*F*	*P*
Races	2	6·35	3·18	3·18	·05
Subjects within races	54	54·05	1·00		
Litters	(3)	(6·75)			
Linear	1	5·76	5·76	7·58	·01
Quadratic	1	·99	·99	1·30	N.S.
Cubic	1	·01	·01	—	N.S.
Races x Litters	6	3·76	·63	—	N.S.
Subjects x Litters	162	123·74	·76		
Total	227	194·65			

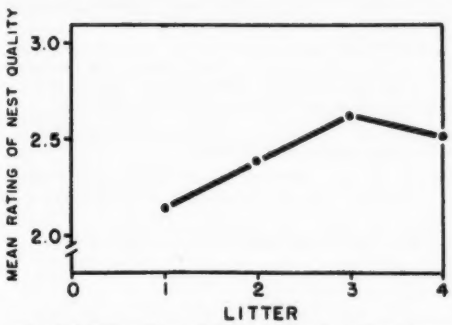


Fig. 4. Mean rating of nest quality for all subjects (N=84) for the first four litters.

In general, then, our analysis has shown significant improvement in quality of nests constructed by rabbits of different races over the first four litters produced.* Figure 4 presents the graph of the overall weighted means of the three races and two sublines. These values were computed from the data presented in Table I.

We have not discussed the strain differences obtained, since this has already been reported (Sawin & Crary, 1953), and the present analyses merely confirmed the earlier findings.

This study was done with the expectation that the previous experience which a mother rabbit had had in building a nest would affect the subsequent nest building. The fact that the curve of improvement (Fig. 4) does not depart significantly from a linear function is supporting evidence for such a view. In accepting such an interpretation, one might assume that the leveling off of the curve after the third litter is an indication that the rabbits had reached an asymptote in the development of this function. This tendency which is observable in three of the genetic strains (Table I) is in line with the known decline in functional activity of the endocrine secretions in later life (possibly with parity). This effect is especially evident in race X. Sawin & Crary (1953) have shown other variations in nesting behaviour, particularly in time for this race. The possibility of a major influence of endocrine balance must be considered. Further, it is possible that these litter changes can be influenced by one or more other variables still to be examined (e.g. temperature at parturition, maternal age, litter size, etc.). Consequently we make no attempt here to interpret, but mainly to document this observation. Further analysis of data already in hand and experimental tests of these interpretations are planned or in progress.

*Because of the unequal N's in the various races an objection might be raised about this analysis, since the overall litter means are weighted as a function of the N for each race or subline. The reader might be interested in knowing whether this finding holds up when each of the races or sublines receive equal weighting. To test this notion an analysis was performed using the 20 mean scores presented in Table I. This analysis gave equal weights to each of the races and sublines. The sources of variance here are: races and sublines with 4 *df*, litters with 3 *df* (analysed into linear, quadratic, and cubic components), and remainder with 12 *df*. This analysis found a significant linear effect at the 1 per cent. level and a significant quadratic effect at the 5 per cent. level. It substantiates the findings concerning the linear trend, and also indicates that the decline in the curve at the fourth litter may not be a random fluctuation but a real effect.

Summary

This study deals with the effects of repeated litter production on one aspect of nest building behaviour, quality of nest. The results in the files of the Rabbit Genetics Laboratory, R. B. Jackson Memorial Laboratory, Bar Harbor, Maine, on over 800 rabbits of different races and sublines were utilised. From these extensive data, a group of 84 rabbits, selected on the basis of having produced four litters, were analysed. They were members of three different races and two sublines as follows: Race X, Race AcEp, Race III, and sublines IIIc and IIIr2.

The hypothesis tested in the analysis was that there would be systematic improvement in performance with each of the four litters in the quality of nest production. Analyses of variance were made, which support the following conclusions: (1) a confirmation of the previous findings by Sawin & Crary (1953) of significant race differences; (2) significant improvement in quality of nest over the first four litters produced; (3) a good approximation of the functional relationship of nest rating to litters, as a linear one. The interpretation of this relationship is quite complex. Both learning and endocrine changes are possible hypotheses to be considered though no conclusion concerning the underlying mechanism is possible at this point. Further analyses and experimentation will be necessary to gain an understanding of this phenomenon.

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PROCEEDINGS OF THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR

At the Annual General Meeting of the Association held in the Department of Psychology, Birkbeck College, Malet Street, London, on Tuesday, 14th February, 1956, the following papers were read. The President, Dr. N. Tinbergen, was in the Chair.

SOME EFFECTS OF SEVERE HYPOTHERMIA IN BEHAVIOUR

By R. W. RUSSELL

Department of Psychology, University College, London

Two experiments were designed to study the effects on two aspects of behaviour, learning and memory, of reducing the deep body temperature of non-hibernating, homoiothermic animals. In the first experiment, two groups of rats were subjected to identical treatment except that the deep body temperature of one group was lowered to between + 1° and 0° C. prior to the time when both groups began learning a serial problem-solving task. The second experiment employed three groups of animals: a control and two experimental groups. The deep body temperature in one of the experimental groups was reduced to between + 13.4° and + 18.5° C. and that of the other between 0° and + 1° C. Except for the "hypothermia" phase of the design, all groups in this second experiment received identical treatments in the following order: training on a maze, hypothermia, tests for retention of maze habit, and training on a serial problem task.

The results may be summarised as follows: animals whose body temperature had been lowered to between + 1° and 0° C. showed a significant impairment in problem solving performance when compared with control animals. On the other hand, no significant differences were found between the performances of control animals and those cooled to between + 13.4° and + 18.5° C. As with such physiological processes as heartbeat and respiration, approximately + 15° C. appears as a "crucial point" below which performance of later tasks is impaired. Our results suggest that this effect may be temporary, since the per cent. of impairment decreased as the interval between body cooling and learning increased.

The results of the retention tests show a consistent trend towards poorer retention after hypothermia, but the differences between experimental and control groups are very small and in no instance statistically significant. The suppression under hypothermia of electrical signs of brain activity and of physiological processes such as heartbeat, circulation and rdspiration appears to have little or no effect on memory. This fact is difficult to explain in terms of a "dynamic" physiological model in which long-term memory is dependent upon the continuous normal activity of the central nervous system.

HEREDITARY DETERMINANTS OF SOCIAL DOMINANCE IN THE GOLDEN HAMSTER

By M. M. LAWLOR

Department of Psychology, Bedford College, London

Although the theory that heredity determines at least in part behavioural differences within species has been subject to experimental investigation since the early part of this century, we still know comparatively little about it beyond the repeatedly demonstrated fact that such hereditary determinants exist. It is suggested that one of the reasons for the relatively slow growth of knowledge in this area is that the problems are particularly complex and demand an interdisciplinary approach which raises its own special difficulties. The use of inappropriate gentic methods, or naivety in the selection and measurement of behaviour variables, have served to limit the significance of many experimental studies.

The experiments described in this paper were carried out in an attempt to determine whether differences in social dominance among golden hamsters could be attributed to genetic factors.

The preliminary study of dominance behaviour is briefly summarised, the main purpose of the paper is to describe the differences observed between two pure bred varieties of hamster (the normal golden or agouti and a cream mutant), and among the cross-bred progeny of these strains.

In general, the findings support the contention that behavioural and physiological characteristics may be genetically linked with coat colour. Animals of the golden strain are dominant over the cream variety. Association with coat colour is emphasised by the fact that, while there is no demonstrable difference in dominance between the homozygote goldens and the herterozygotes who carry the cream recessive, both the homozygote and herterozygote goldens are dominant over the creams. The differences are observed in the cross-bred animals but are rather less conspicuous, this suggests that modifiers, established by selective breeding within the strains but not linked with the colour genes, also exert some influence on social dominance and may be to some extent responsible for variations in such dominance within the varieties. An attempt is made to relate these results to general theoretical principles.

DEVELOPMENT OF RUMEN PAPILLAE IN CALVES FED WITH DIFFERENT DIETS

By A. BROWNLEE

Agricultural Research Council Field Station, Compton, Berkshire

Twenty-four calves, all about a week old were divided into four groups and fed as follows :

Group (I) milk and milk-substitute.

Group (II) milk and milk-substitute + hay.

Group (III) milk andmilk-substitute + grass.

Group (IV) milk and milk-substitute + concentrates (proprietary calf-pencils)

All were bedded with peat-moss litter. The calves in group (1) ate some peat and on post mortem a quantity of peat was found in the rumen in every case. The other calves were not observed to eat peat and peat was not found in their rumen.

All calves were destroyed after twelve weeks on the experiment except three calves in group (I) which showed tetany; one died at 55 days and two were destroyed at 72 and 78 days respectively.

The rumen papillae were undeveloped in group (I), more developed in group (II) and most developed in groups (III) and (IV). The average wieght of the whole of the rumen mucous membrane (after being stripped by manipulation from the muscle coat) expressed as a percentage of the average live weight was:

Group (I) 0.224%
Group (II) 0.496%
Group (III) O.702%
Group (IV) 0.826%

The epithelium in the case of the concentrates group was relatively fragile on manipulation, whereas that in the hay and grass groups was relatively tensile.

The order of development of papillae in the peat, hay and grass groups is directly as the order of food preferences for these three substances. Development of rumen papillae is apparently not pre-determined.

NEST CONSTRUCTION IN THE WEAVER BIRDS WITH ESPECIAL REFERENCE TO THE GENUS QUELEA

By JOHN H. CROOK

Madingley Ornithological Field Station,, Department of Zoology, University of Cambridge

Colonial Weaver birds (*Ploceinae*) construct nests of two principal types, the Pendant and the Globular, of which the former hangs from a single knotted attachment to a twig and the latter has the supporting twigs incorporated within the walls of the structure. In the two cases a pendant loop or an initial ring are formed first respectively and the lower edges of these are used in each case as a perch from which the nest chamber and entrance funnel are constructed.

Observations made at Madingley and in Senegal on the nest building of *Quelea quelea*

quelea in aviaries show that the nest enlarges by a constant repetition of an Act Sequence performed by the male bird. Each sequence is characterised by the following acts: grass cutting, termination, stitching, and often shaping and/or titivation. After the completion of a stitch there is a pause before the occurrence of the next sequence. The sequences show an increase in complexity with the growth of the nest and wane into mere titivating when the structure is completed.

The stitches, of which three principle kinds, knotting, twining, and weaving have been distinguished, are apparently determined by the stage of construction of the nest. Males may build on more than one nest at the same time (under aviary conditions) and use the appropriate stitches at sites holding nests at very different stages of elaboration.

The whole building tendency in Cambridge was very much depressed when compared with that observed in the Senegal. Although stitches were identical, nests in England never became fully elaborated structures and were never destroyed after completion by the continuance of titivation upon the dried and brittle materials of the nest.

BACKGROUND-SELECTION IN TADPOLES OF *Xenopus laevis*

By MARGARET R. WHEELER

Department of Zoology and Comparative Anatomy, University Museum, Oxford

Tadpoles of *Xenopus laevis* were kept on either a black or a white background until all melanophore changes were complete. Then, one at a time, they were offered a choice between these backgrounds and their movements observed for several minutes. One hundred and sixty-one out of one hundred and ninety-six white adapted tadpoles chose white and one hundred and twenty-eight out of two hundred and three black adapted tadpoles chose black. Animals on the "wrong" background showed signs of disturbance. When a tadpole is on a background appropriate to its melanophore state it is relatively inconspicuous. Therefore, the behaviour recorded above probably reduced the risk of predation.

It seemed possible that the output of 'B' and 'W' hormones which controls the melanophores might also regulate the selection behaviour. Alternatively, the behaviour may be independent of the colour change; or, an animal's colour, determined by its melanophore state, might control its movements. White adapted tadpoles were injected with 'B' hormone in order to turn them black. These animals chose white, therefore, animals cannot be selecting their background according to the state of the melanophores, nor can the presence of 'B' hormone be determining the choice of black. Possibly an animal chooses white in the presence of 'W' and black in its absence. This is unlikely, for it is improbable that 'W' is secreted in animals which have been kept in total darkness, yet such animals prefer white. It seems that background selection and colour change are independent.

This work was done whilst in receipt of support from the Agricultural Research Council.

An Ordinary Meeting of the Association was held in the Department of Psychology, Birkbeck College, Malet Street, London, W. C. 1., by kind permission of Professor C. A. Mace, on Wednesday, 19th October, 1955, at 2 p.m. The following papers were read.

A STUDY OF LIBIDO DIFFERENCES IN COCKERELS

By D. G. M. WOOD-GUSH and R. OSBORNE
Poultry Research Centre, Edinburgh

The mating frequencies of 30 cockerels were studied under uniform conditions. These males belonged to six sire families and 15 full-sib pairs. It was found that there were significant differences between the sire families, indicating that mating frequency has a genetic basis. When incompleted and completed matings were weighted, these genetic differences remained and the use of a discriminatory analysis showed that the frequency of all types of mating was the best criterion of individual behaviour.

During the course of mating frequency tests, monthly samples of semen were taken from the males. No correlation was found between the mating rank of a male and the quality of his semen assessed on volume, density and sperm morphology.

The five top ranking and five lowest ranking males were tested for fertility and the top ranking males gave the best results as a group.

A significant negative correlation (—0.4303) was found to exist between comb height and mating frequency. Furthermore, there was a correlation of —0.5055 between mating frequency and comb index (=height/width) calculated from the 15 dam-family averages of these variables and one of —0.6368 from the 6 sire-family averages. Further analysis revealed the apparent absence of genetic variability in comb index suggesting that the correlations were phenotypic only and indicating that the differences in mating activity could not be wholly explained on the basis of comb index. Finally dubbing failed to improve the mating frequency of two low ranking cocks to any great extent.

SOME EXPERIMENTS ON THE FOLLOWING AND THE FLOCKING REACTION OF MALLARD DUCKLINGS

By U. WEIDMANN
Department of Zoology, Oxford

My own work, done three years ago, based mainly on Fabricius, (1951) admirable study which in turn was inspired by Heinroth's (1910) discovery and Lorenz's (1935) discussion of the *imprinting* process.

The analysis of the following (and the flocking*) response involves: (1) an investigation of the *very first* "inborn" response (i.e. what *stimuli* release it, how do age and different circumstances influence the chick's *responsiveness*?), and (2) an investigation of the subsequent *change* of the response (i.e. what does this change *involve*, how is it *established*?).

Before the experiment ducklings were kept isolated and were fed in special boxes. The same releasing stimulus-situations were found as reported by Fabricius for other duck species.

*Flocking denotes a following response directed towards other ducklings instead of towards the parent. Otherwise the two were found to be similar.

An imitation of the leading call of a mother duck may be a better stimulus than quickly repeated short calls but more experiments are needed. The existence of a *sensitive period* (after which ducklings would not follow or flock, if they had never done so before) as claimed by Fabricius, was confirmed for well-fed ducklings, too. This period was not due solely to an increasing escape tendency inhibiting the following: 40-hour old ducklings though not frightened would not react any more when called.

After following for about half an hour, the response undergoes some striking changes: its *selectiveness* is increased (i.e. the object followed hitherto is preferred), whether *irreversibly* has never been adequately tested. Its *readiness* si enhanced and it can occur *far beyond* the sensitive period. This is not due to reinforcement alone (e.g. getting food) as fully

isolated ducklings would follow 1 week later after only 30 minutes' following experience.

The underlying process takes a *brief time* and does not occur at the beginning and the end of the sensitive period; best imprinting age is 16 hours (Ramsay & Hess, 1954).

Fabricius' theory on imprinting was discussed. He overlooks the great *difference in responsiveness* between a non-imprinted and an imprinted duckling: in the *absence* of all (complicating primary and secondary) releasing stimuli (see Fabricius) the imprinted duckling stops other activities and *searches*, the non-imprinted one (even if tame) shows no such appetitive behaviour; it has lost (or never *gained*) this urge to be near a parent.

A NOTE ON THE LIGHT SENSITIVITY OF BLIND CAVE FISHES

By G. THINES

Laboratory of Zoophysiology, University of Louvain, Belgium

In a recent revision (Thines, 1955) it was found that there exist about 40 known species of blind freshwater fishes belonging to eleven families, most of them living in caves. These fishes are generally depigmented and there seems to be some genetical correlation between pigment-loss and eye-loss. The eyes of the adults consist of degenerated morphological remnants, disorderly arranged, which have receded inside the skull and are covered by skin. The size of these structures, relative to the total size of the head, is considerably smaller than in normal eyed Teleosts. In that state, there remains no possibility of an optical image being formed whatsoever.

If it can be admitted that the possession of a differentiated image-forming eye is of no biological use to fishes living permanently in a completely dark cave, that of a diffuse extra-ocular sensitivity to light might on the contrary be extremely useful to them in providing them with information on the limits of their biotope. If they display a photonegative reaction, they will be thus prevented from swimming astray into lighted zones outside the cave, where they would meet strong biological competition, namely the form of eyed predators in which, in the long run, would cause their extinction (cf. Eigenmann, 1909).

Experiments on the extra-ocular sensitivity of two species of blind cave fishes, *Caecobarbus geertsi* Blgr (Cyprinidae) and *Anoptichthys jordani* Hubbs & Innes (Characidae) show that they display a photonegative reaction (Breder, 1944; Breder & Rasquin, 1947; Thines, 1953, 1954). The fishes react to a difference of brightness even of a very small degree (less than 1 lux) (Kuhn & Kähling, 1954; Thines, unpublished data), but show no spectral praeferendum. These findings fit in with the general light conditions of a cave entrance, where differences in wavelength can be considered as unimportant.

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SPEECH COMMUNICATION BETWEEN HUMAN BEINGS AND DOGS

By G. J. RENIER

University College, London

For nine years I have tried to use as a means of communicating with a standard poodle dog and a dachshund bitch a simplified form of human speech, from which I eliminated all grammatical inflections and all words that could not conceivably convey any kind of signal to the dog. The poodle was under constant observation by myself and my wife for eight years, the dachshund for two. An attempt was made to divest our verbal communication of overtones of sentiment and of any of the non-linguistc signals that are so easily interpreted correctly by dogs. I call this the "verbalisation" of contacts. I made the following observations:

1. The extensive generalisation of which dogs are capable could be made to centre upon verbal signs like "garden," "dish," "stick," "ball," "little-girl," "car," etc.

2. I found that verbal instructions or hints could be conveyed to the dogs, but particularly to the poodle, by which they were induced to think or to reason, and by this I mean that they were led to compare a present situation with memories of past situations and to act upon the result of this comparison. The poodle who "knows" the words water, ball, fetch is presented with the novel situation of being told "Fetch ball in-water." He jumps into the river, rescues the ball, presents it to his master. He is then told (other novel situation): "Give ball to-little-girl," whereupon he goes to her at once and drops the ball at her feet. Neither order has to be repeated.

3. I was able to make the poodle distinguish between statements about different moments in the future. This was done not by training or drill but by using as often as possible in the right connotation the words "soon," "later," "tomorrow." To the toneless statement "Olive come back soon" he reacted by going to the window at once to look out for the return of his mistress. The statement "Olive come back later" brought no immediate reactions, but the observation post was occupied without prompting after about thirty minutes. (Reaction of similar nature to the statement "walkies later"). The statement "Olive come-back tomorrow," made in the evening led to no reaction, but next morning the observation post was occupied without prompting. The dachshund bitch is beginning at present to distinguish between "soon" and "later," but it is too early to be certain of this. It would also appear to be possible to convey understandable reference to the past by using the auxiliary verb "been"; "Ricky been walkies." Some experiments tend to show that the poodle did not take "been" as some unusual way of saying "no" but realised its proper reference to a recent past.

DISCRIMINATION LEARNING AND MOTIVATION*

By H. M. B. HURWITZ and J. ROWELL
Birkbeck College, University of London

The part played by *degree* of motivation on the learning rate and strength of a discrimination was investigated in a composite experiment using rats in a water maze.

Two groups, A. and B, of male rats were detained in water for 10 seconds and 40 seconds respectively, before being permitted to make a discrimination, i.e. selecting the brighter of two doors in order to gain immediate access to a safety platform. In this way, *degree* of motivation during discrimination learning could be controlled. The *rate* of learning was assessed in terms of the number of trials required to make five successive, errorless discriminations. The *strength* of the discrimination was measured by a reversal test, i.e. the number of trials required to reverse the significance of the discriminable cues. During this test both groups were detained for 25 seconds.

Both groups learned the original discrimination at the same rate. However, the results show that the high drive group (Group B) were more ready to reverse the discrimination than the low drive group, the difference being statistically significant at the 1 per cent. level.

At first glance these findings conflict with certain well established generalisations about conditions favouring discrimination learning: that the speed of mastering a problem is closely linked to degree of motivation (drive-strength) and that the stronger a habit the more difficult its subsequent reversal. The conditions of our experiment might be expected to favour a stronger discrimination habit for Group B, so that the actual results came as a complete surprise.

It seems, at first sight, that our results and the above generalisations could be reconciled by denying that the different detention periods effectively produced different drive-strengths: it should then follow that both groups would acquire the discrimination equally rapidly and well. We have rejected this as a complete interpretation on two counts: (*a*) there is evidence that the discrimination was mastered to different extents, as shown by the more rapid reversal of Group B. Since all other factors were kept constant, this difference must be attributed to the effects of long vs. short detention; (*b*) observations showed that each detention period was effective in promoting a distinct method of

*A more detailed description of the experiment reported here will shortly be published under the title "Drive-strength and adaptation to stress."

coping with the stress situation. Group B learned to remain perfectly motionless and apparently relaxed when placed into the water: Group A was paddling actively throughout the short detention period. We have therefore argued that two distinct forms of learning occurred in the course of the experiment: (1) firstly, adaptive responses to stress which function to minimise strength drive; (2) secondly, a discrimination on the basis of which an immediate escape from the water tank could be accomplished.

Furthermore, the more rapid reversal by Group B may be accounted for in terms of their superior adaptive skill, based on more extensive experience of water-immersion.

SOME EFFECTS OF PRE-TRAINING ON SUBSEQUENT SHAPE DISCRIMINATION IN RATS

By P. C. DODWELL

Birkbeck College, University of London

A brief outline of Deutsch's theory of shape discrimination was given. This theory accounts for Lashley's finding that rats fail to discriminate a square from a circle of equal area and brightness.

An experiment with twelve rats was performed, to confirm whether the square/circle and diamond/circle discriminations are possible, and to determine whether the discriminations, when learned, are due to response to an isolated element of one of the shapes.

The rats were pre-trained to discriminate a grid of horizontal from a grid of vertical lines, on a modified Lashley jumping stand. They were then divided into equated groups, and taught various discriminations.

The results show that under the given conditions square/circle discrimination is possible, the rate of learning depending on the size of the presented shapes. There is transfer to a variety of shapes having one distinct element in common (horizontal base line). No transfer was obtained to any shape without this element.

Diamond/circle discrimination was not obtained.

Square/pentagon discrimination was obtained but there was no transfer from square to circle, which would be expected if these shapes are confused with one another.

The main conclusions drawn are: that rats can learn to discriminate square from circle under certain conditions of pre-training; that discriminations are largely affected by pre-training on a shape discrimination; and that shape discrimination may be attained by isolation of an element of one of the shapes, an effect which persists even when the shapes are small enough to present a narrow visual angle, and therefore presumably fall within the rat's field of distinct vision. This last fact constitutes a serious objection to the theory mentioned, as it stands at present.

BOOK REVIEWS

The Physiology of Domestic Animals. By H. H. DUKES. London: Baillière, Tindall & Cox Ltd. 1955. Seventh Edition. Pp. xii + 1,020, 238 illustrations. 80s.

A new edition of this well-known and widely used textbook has been badly wanted for several years, and its appearance is most welcome. The author has again wisely incorporated chapters by a number of specialist workers, and with the addition of M. R. Kare (chapter on "Water, Electrolytes, and Acid-Base Balance") and J. A. Dye (three chapters on intermediary metabolism) to the list of contributors the book takes a further step towards an edited work. An appendix on "Lecture Demonstrations in Physiology" is a further innovation, while the number of illustrations has been increased from 184 to 238.

The expansion of the text has clearly been based upon considered revision rather than upon mere additional matter. Indeed, with the appearance since the previous edition of Sturkie's *Avian Physiology* and Albritton's *Standard Values in Blood*, some of the previous tables have been curtailed and references given in their place to these specialist works. The citing of new references in full, with title is a welcome feature, and "Dukes", although designed originally for veterinary students, must be regarded as of growing value to all, including research workers, who are interested in veterinary and comparative physiology. It should be accessible to all who are concerned with problems of mammalian and avian behaviour.

A.N.W.

Keeping and Breeding Aquarium Fishes. By C. W. EMMENS. New York: Academic Press Inc. 1953. 202 pp. 36s.

Written primarily for aquarists specialising in tropical fish, this book contains practical information on the up-to-date application of general principles of aquarium management and fish breeding which are too often misunderstood, or disregarded from familiarity, yet are of vital importance to keepers of any kind of fish, for any purpose. Tank capacity, water qualities and aeration are among topics dealt with and in regard to the setting up and furnishing of tanks the book is refreshingly free of "notions." The chapter on foods and feeding is of special interest since it includes recent useful additions to the traditional fish foods and mentions antibiotics—with a word of caution that knowledge of their long-term effects is at present scanty. Special chapters deal with the breeding habits of particular Tropicals and care of the fry. The book is illustrated with photographs and diagrams. The London-born author is Professor of Veterinary Physiology at the University of Sydney, New South Wales.

E.M.B.

Birds as Animals, Vol. I. History of Birds. By JAMES FISHER. London: Hutchinson. 1954. Pp. 184. 8s. 6d.

"Birds as Animals" was the title of an earlier work by Fisher. Roughly half of the subject matter considered in this book has been dealt with and re-written in the new one. A second volume, entitled "Migration and Habits" is in preparation. The present book constitutes a history of ornithology from the Old Stone Age to the present time. To quote from the descriptive note inside the dust cover, "the new book is the first part of an essay on the bird's place in the animal kingdom" and "the author returns to a critical synthesis of the zoology of birds." Again, "the title of the book has been deliberately chosen to remind the reader that ornithology is a vital part (of growing importance) of the study of the animal kingdom". The first three chapters deal, in general terms, with the growth and development of the study of birds and provide an informative introduction to more specific topics discussed in the remainder of the book. These topics include a chapter on geographical distribution from which we learn, at the outset, of the achievements of early observers in the statement that "about 90 per cent. of the birds in the world had been discovered and described by 1850." In discussing the history of the bird, the author tells us that "it is now possible to see the adaptive radiation of the bird in the Cainozoic era as a phenomenon of the same calibre as any other great revolution in vertebrate evolution, like the conquest of the land by the amphibian." Later, the intricate question of speciation is discussed. The last three chapters are of particular interest to the non-specialist reader in that they afford a glimpse of less familiar lines of enquiry and the trends in contemporary investigation. These chapters are concerned with absolute and comparative

numbers of birds, the effect on bird populations of changing environments; these matters are appropriately rounded off in a final chapter dealing with the influence of man's activities on bird numbers. A comprehensive bibliography and index complete a work of considerable scholarship and importance.

C.H.-S.

The Ring. Edited and published by DR. W. RYDZEWSKI. Quarterly, 4/-

This carefully edited bulletin is devoted to ringing, especially the technical aspects such as ring design and systems of administration. International in scope and content, it fosters co-operation between the various ringing schemes. The review copy, No. 5 (22pp.) includes brief histories of Canadian and American ringing schemes, a detailed analysis of ring inscriptions, a discussion on the publication of recoveries, a longevity table, current reports and news from a number of countries and a useful classified list of recent literature in which east European publications are well represented.

R.S.

BOOKS RECEIVED

The following books have been received, and in appropriate cases will be reviewed as space permits in early issues:

A. R. Michaelis (1955)
Research Films in Biology, Anthropology, Psychology, and Medicine
New York: Academic Press Inc. $10.00

Ian Harman (1955)
Finches
Wisconsin: All Pets Inc. $4.00

L. Fisher, Ed. (1955)
Marine Tropicals
Wisconsin: All Pets. Inc. $1.50

Stuart Smith & Eric Hosking (1955)
Birds Fighting
London: Faber & Faber 18s.

S. H. Skaife (1955)
Dwellers in Darkness
London: Longmans Green & Co. 25s.

Tracey Storer & Lloyd Trevis Jr. (1955)
California Grizzly
University of California Press 56s. 6d.

BIRD STUDY

The Journal of the British Trust for Ornithology

Edited by H. N. SOUTHERN

Contents of Vol. 3, No. 1, (March, 1956) include: *The Iberian Peninsula and Migration*, by R. E. Moreau; *The Significance of Some Behaviour Patterns of Pigeons*, by Derek Goodwin; *Seaward Flights of Swifts at Dusk*, by David Lack; *Report on the National Census of Heronries 1954*, by J. F. Burton.

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The Elephant Seal

(*Mirounga leonina* Linn)

A series of illustrated monographs by R. M. Laws, M.A., Ph.D., of the National Institute of Oceanography, published under the auspices of the Falkland Islands Dependencies Survey in their series of *Scientific Reports*.

Part I.	**Growth and Age.**	(*Scientific Report No. 8.*)	20s. (post 7½d.)
Part II.	**General, Social & Reproductive Behaviour.**	(*Scientific Report No. 13*)	30s. (post 8½d.)
Part III.	**Physiology of Reproduction.**	(*Scientific Report No. 15.*)	In preparation

Two further reports on the Elephant Seal are planned for this series.

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Zeitschrift für Tierpsychologie is published in yearly volumes of three numbers which appear irregularly. Each issue contains about 160 pages and costs approximately DM 35.0 (£3). Single copies may be purchased separately.

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3

NORMAL AND IRRELEVANT TOILET BEHAVIOUR IN *Emberiza* Spp.

By R. J. ANDREW

Madingley Ornithological Field Station, Department of Zoology, University of Cambridge

Toilet behaviour is behaviour directed to the care of the body surface. Other responses such as stretching and yawning, are often associated with it in birds, and are also considered here. Toilet behaviour has afforded a disproportionately high number of examples of "displacement activities" (irrelevant behaviour; Tinbergen, 1951). Since it now seems probable that peripheral stimuli are of critical importance in the causation of some irrelevant behaviour (e.g. Andrew, 1956), a study in a single group of the causal factors of normal toilet behaviour, and of its irrelevant occurrences, seems likely to be of value.

The species chosen were *Emberiza citrinella* (Yellowhammer), *E. calandra* (Corn Bunting), *E. schoeniclus* (Reed Bunting) and *E. tahapisi goslingi*. Their behaviour was so similar that, in general the following account does not distinguish between them.

1. Description

A. Preening. The feathers are smoothed and cleaned by being drawn through the bill (Nice, 1943). The body feathers are often slightly raised, sometimes due to a weak tendency to give feather-settling movements (below), and sometimes because the bird is preening in a resting attitude. They are also raised as part of the preening movements themselves, for instance when taking oil from the uropygial gland.

B. Scratching. The sides of the head, and occasionally the crown, are scratched with the foot, which is passed between the wing and the body.

C. Feather-settling Movements

(a) General descriptions. The complete form of these movements usually only occurs after bathing. The feathers are somewhat fluffed, and the wings begin to vibrate more or less horizontally out from the sides of the body, in a movement which involves little extension. The forebody may be slightly lowered. Sometimes during a very brief pause in the vibration, the whole wing is hitched higher on the bird's back, and the wings vibrate more or less vertically upwards, still with no great extension. Occasionally such a vibration is so strong as to lift the bird into the air. After this change in the wing vibration, a lateral shaking of the body usually begins, during which the wing vibration is often less intense. Usually at the same time the body feathers are raised further, and the tail is shaken laterally and spread; this last component may also occur independently of the body shaking. Towards the end of the body shaking, the neck is usually extended slightly forwards, and the bill may be turned slightly downwards in one or two nodding movements. The wing vibration and the body shaking then cease, the feathers return to normal, and the head is drawn back. Such a feather-settling may last 5 seconds or more.

In more incomplete feather-settlings, the wings are vibrated without any change in direction, either horizontally, or rarely in a direction intermediate between the horizontal and vertical; these, too, end with body shaking. Feather-settlings given when the plumage is dry, are usually incomplete in that the wings are only vibrated slightly (or not at all), and the tail is not shaken.

(b) Low intensity feather-settling wing movements. A low intensity wing vibration may be given very persistently when the wings are damp, without apparently interfering with such activities as feeding or locomotion. In the commonest form the wing is in a position through which it never passes in the full intensity feather-settling wing vibration. It is drooped* and very slightly vibrated, with movements of both extension and elevation; at a lower intensity still the wings may be drooped and motionless. The drooping seems to occur because the wings, slightly raised and so deprived of support of the flank feathers, are allowed to sink under their own weight. They may be repeatedly hitched a little higher, and then allowed to sink back more slowly. The wings are sometimes trailed* during preening, and occasionally they are also laterally vibrated. All these variations in form and

*A drooped wing sinks downward at the tip, with little or no elevation but some splaying apart of the primaries. A trailed wing differs in lacking this splaying.

intensity (except those due to a division into horizontal and vertical phases) may occur in the apparently unrelated courtship wing vibrations (Andrew, in press).

Wing-hitching is sometimes common when the feathers are damp. The movement slides the wing high on the back so that they meet or overlap, and is almost identical with the hitching which occurs between the two phases of feather settling wing vibration. Derivation from the latter movement would explain why such hitching never happens during a tendency to give courtship wing vibrations (which are not divided into two phases). The hitching movement is not given if the bird remains quite still, but only if it moves about now and then.

(c) Low intensity form of other components. A slight fluffing of the feathers, and extensions of the neck are the components given at the lowest intensities when the plumage is almost dry (see experiments below). Sometimes the fluffing is held for some time, and sometimes the feathers go up and down several times quite rapidly before full feather-settling is given. Often fluffing, neck extension, nodding and a slight lateral head shake, are the only components given when feather-settling is being used to smooth feathers disarranged by preening.

D. Bathing and Drying

(a) Bathing. Bathing movements consist of two alternating phases, which are usually given whilst standing in water. In the first, the bird pecks into the water, and often makes sideway strokes with the bill which throw up water. At the same time, or after a few pecks, the wings begin to beat outwards from the body in one or more bursts. In the second phase, the body is raised to its normal position and the wings are hitched so high on the back that one wing tip overlaps the other. The uppermost wing begins to flick rapidly in a vertical direction. Often, after a little there is a momentary pause and the two wings change position. Sometimes the undermost wing beats slightly; occasionally the wings do not overlap properly and then both wings seem to beat. Water is shaken off the wings, much of it falling clear of the body. During both phases of bathing, the body feathers are somewhat raised and the tail may be spread.

Emberiza cttrinella and *E. calandra* exchange the position of their wings less often during a single second phase of bathing than *E. schoeniclus*. In one series of observations *E. calandra* and *E. schoeniclus* exchanged their wing positions on the average 0.7 and 2.6 times respectively, so differing very significantly ($p < .001$ on a t test.)

Unlike other wing vibrations those of bathing and of feather-settling are given in two phases (the first directed horizontally outwards, and the second vertically upwards with the wings hitched high on the back), and so are probably homologous. *Emberiza* species use sideways blows of the bill to turn over material when searching for food, which may be homologous with the similar movements of the first phase of bathing.

(b) Active drying. This consists of intense feather settling-movements in which wing vibration and tail shaking are emphasised. In the water, it alternates with bathing movements, and after bathing with preening of the primaries (in which alternate wings are often preened in each succeeding bout). In the analysis of toilet behaviour sequences (see below) feather-settling with marked wing vibration (as opposed to feather-settling without), is very significantly associated with preening the primaries (as opposed to preening the rest of the body), ($p < .001$ on χ^2_1). Later, in drying, other parts of the body are preened, particularly the rectrices.

Oil is often taken from the uropygial gland during the period of drying, and the head is often rubbed on the shoulders, a movement which probably transfers oil to the side of the head.

(c) Passive drying and sunbathing. Passive drying usually appears some time after bathing, although occasionally the bird will sit in the water in this attitude. It crouches in a resting attitude with its wings raised a little, or drooped, or trailed, its feathers somewhat raised, and often its tail widely spread. Slight tail shaking and wing vibration sometimes occur.

A similar posture is given in sun bathing, usually with the addition of the body cooling responses of panting respiration, and sometimes gaping. The wings are often slightly splayed at intervals, which suggests that there may be a tendency to give a feather-settling wing vibration. The tail may be spread and deeply drooped.

E. Bill-wiping and the Rejection Movement

In bill-wiping, first one side of the bill, and then usually the other is wiped over the perch

from its base to its tip. The rejection movement, which is used to remove material from the mouth, consists of a strong lateral shaking of the head with the bill somewhat open, and often alternates with bill-wiping.

F. Pecking

The bird tries to peck off new leg rings, or clots of dirt on body or feet. Dry droppings round the vent are usually pecked away.

G. Yawning

The bill is opened wide and usually tilted a little upwards.

H. Stretching

The Buntings possess the same three main stretchings as *Melospiza melodia* (Nice, 1943). In the first, the wing and leg of the same side are stretched laterally, and the tail is spread on that side only; occasionally the wing on the other side is slightly raised. In the second, both wings are stretched upwards with very little extension. The tail is not spread. In the third rarer type both legs are stretched, and the wings are extended downwards with no elevation. The whole of the tail is usually spread. The similar movement in *melodia* was given only by the fledglings. Adult Buntings occasionally gave it, although it was most common in Reed Bunting fledglings.

A sideways stretching of the wing and the leg is usually followed by a stretching of both wings upward.

2. Statistical Analysis

Records were made of series of toilet behaviour and other responses in *E. citrinella* and *E. calandra*, and all were lumped together in order to obtain sufficient data for a rough statistical treatment. The series were divided into units at the points where a particular response ceased; thus a preening unit ceased when the bird paused at the end of preening a particular area, and bill wiping units usually ceased at a pause after wiping both sides of the bill. The statistical method is described in the legend to Table I, which contains the numerical results.

Table I. Toilet Behaviour Sequences in Emberiza Spp.

		Followed by ——>							
		Scratch	Preen	Feather-settling	Stretch	Yawn	Bill wipe	Loco-motion	Rest-ing
Precedes ↓	Srcatch	1 0·66	6 5·4	3 2·2	— 1·5	2* 0·28	1 1·7	— 0·99	— 0·33
	Preen	7 5·6	74* 45·8	22 18·3	6 12·2	— 2·3	—* 14·5	1 8·4	— 2·8
	Feather-settling	2 1·8	13 14·6	7 5·8	3 3·9	1 0·74	2 4·6	5 2·7	2 .89
	Stretch	— 1·4	2 11·7	— 4·6	13* 3·10	— 0·60	1 3·7	9* 2·1	3 0·71
	Yawn	1 0·26	1 2·1	— 0·83	— 0·55	2* 0·11	— 0·66	1 0·38	— 0·13
	Bill wipe	1 1·9	1* 15·5	5 6·1	1 4·1	— 0·79	26 4·9	2 2·8	1 0·95
	Loco-motion	— 0·20	1 1·7	2 0·66	— 0·44	— 0·08	1 0·53	— 0·31	— 0·0
	Resting	— 0·15	— 1·2	— 0·50	3* 0·33	— 0·06	— 0·40	— 0·23	— 0·08

The behaviour patterns are described in the text. The upper figure of the two in each cell is the obtained total occurrences, and the lower is the expectation. The square root of the latter was used as a rough estimate of the standard error of the obtained total (I am indebted to Dr. H. E. Daniels for this statistical method). A difference of more than three times the standard error between the obtained and the expected totals was taken as significant. The cells which indicate significant associations are asterisked.

Preening, stretching and bill-wiping tended to be followed by themselves. Stretching tended to be followed by movement, scratching by yawning, and resting by stretching, (the last two results were based on too few figures to be more than suggestive). (As a result of these positive associations, some negative associations also occurred). There were two main groups of responses, the members of each of which tended to occur together: the first was scratching, preening and feather-settling; the second, stretching, rest and movement. When a two by two contingency table was drawn up for these two groups (excluding all cases in which a particular type of behaviour was followed by itself), it could be seen that behaviour which fell into one group tended to be followed by behaviour of that same group, ($p < .001$ by χ^2_1). Bill wiping appears to be somewhat isolated.

In the next two sections the factors which may cause these and other associations, are discussed.

3. Peripheral Stimuli causing Toilet Behaviour

A. Tactile Stimulation of Body Surface

(1) *Water spray experiments.* Five *E. tahapisi goslingi* were sprayed with very fine droplets of water. In 6/12 cases the first responses included bill wiping, (which was accompanied in one case by the bird slightly opening its bill as if to taste the water drops), in 8/12 slight neck extensions and noddings, and in 4/12, a slight raising of the feathers. These responses appeared almost immediately, which shows that bill-wiping and low intensity feather-settling movements are produced in a reflex-like manner by foreign material on the bill and body feathers. This may be compared with the reflex-like way in which the wing drying movement of *Phalacrocorax carbo* occurs when the wings are heavy (Kortlandt, 1940).

As the spraying continued, wing vibration was added to the feather-settling movements, although it did not appear until the wings were fairly wet; and only after about five minutes did preening and scratching appear.

(2) *General.* When the wings are wet, wing vibration is very persistent; otherwise it only occurs during the actual course of a feather-settling, and then only at low intensity. This, and the spray experiments, suggest that wing vibration is a fairly direct response to wet (or heavy) wings. Preening of the primaries may be a delayed response to this stimulus. This would explain the association between intense wing vibration and primary preening.

Bill-wiping is given in response to any dirt on the bill, as well as water (spray experiments). Oil and scurf will stick to the bill during preening which thus helps to explain why bill wiping occurs in the same period as preening.

Disarrangement of the body feathers often seems to provoke preening.

B. Irritation in the Respiratory Passages

Certain yawning (or gaping) movements appear to be caused by this. In the hiccup, the bird yawns wide, and at intervals the belly is drawn up and the breath blown out. In the sneeze, breath is blown out through the nostrils, followed by forward jerks of the head and slight gapes. Scratching seems to be associated with yawning when there is internal irritation, perhaps in the Eustachian tubes. The bird persistently yawns, raising the head a little; at intervals, it scratches the side of the head and finally may rub it on the perch.

C. Unpleasant Taste

The rejection movement and bill wiping are aroused by pecking into excrement, as if because of its unpleasant taste.

D. Heat

Two out of four *E. citrinella* gave the full pattern of sunbathing as the first response to a rise in the air temperature (experiments, Andrew, 1956). The birds gaped widely and then, after a little, suddenly abandoned the sunbathing and took up the full cooling posture. Morris (in press) has shown that certain Estrildines raise their feathers in response to strong heat from lamps, probably as a cooling response. The *Emberiza* feather raising, on the other hand, was part of sunbathing, and, since in most areas the feather tips were not separated, had probably no cooling value.

Heat is probably one of the factors which cause the almost identical posture of passive drying (above) to appear, since this is often assumed when the bird has found a warm place.

E. Proprioceptive Stimuli

Stretchings tend to follow rest; they are particularly common just after brooding, when the bird has been cramped for some time. Comparison with similar movements in man suggests that they may depend partly on proprioceptive stimuli from long inactive muscles.

4. Other Causes of Toilet Behaviour

A number of the associations between different types of toilet behaviour cannot easily be explained by their being aroused by the same periphal stimuli. Thus the different stretchings (above) tend to occur together and are sometimes associated with yawning; possibly all share a central casual factor* which could be called a tendency to stretch. Similarly a bird which has been able to wet only its head in its attempts to bathe, may give full bathing movements and intense active drying. Here feather-settling wing vibration, and other components of feather-settling, probably depend largely on central factors (despite their direct dependence on peripheral stimuli in other situations). Central factors may be important in causing frequent slight feather raisings during bouts of bill-wiping, and also in causing the persistency of the tendency to bathe: once the tendency to bathe is aroused, a bird may repeatedly approach a water dish despite its fear of a superior perched near the dish.

A factor which is probably important in producing the general association together of different types of toilet behaviour, is the absence of any other strong motivation. Toilet behaviour is easily suppressed by other tendencies. In the midst of bathing a bird will flee a superior, and a bird with wet plumage will not give feather-settling movements for several minutes after being put into an unfamiliar cage. Male *E. calandra* usually sing after flying up to a song perch from ploughland, when the bill and feet are often very dirty; and it is usually only after the first few songs (when, presumably the tendency to sing is weaker), that they are cleaned. It is rare for toilet behaviour to interrupt some other activity. (Occasionally a bird may peck out a loose feather in the middle of feeding).

Stimuli for most of the toilet movements are likely to be fairly continuously, if weakly, present, and such stimuli will become stronger if the movements are not performed for some time. Thus preening, scratching, feather-settling and bill-wiping will tend to occur when other tendencies are absent, and so will tend to be associated. Sleep is probably another activity that tends to appear when other motivations are low, and this would explain why toilet behaviour often occurs in the same period of time as a resting attitude.

Possibly it is because the bird is often rather inactive during periods of toilet behaviour, that they tend to be followed by stretching.

*Used in the sense of causal factors which do not depend in a reflex-like way on particular stimuli external to the CNS (either innately or by conditioning).

5. Irrelevant Occurrences of Toilet Behaviour

A. Preening

(1) *Complete preening. E. schoeniclus* females sometimes preened after giving a distraction display. Between preening they watched the intruder intently. Female *E. calandra* often preened when perched near a male; sometimes they began to preen just as the male flew to them. A male *E. citrinella* which was giving lateral body swings in reproductive fighting (Andrew, in press) twice suddenly preened his wing primaries when his head came close to them at the end of a swing.

(2) *Incomplete preening.* Male *E. citrinella* sometimes lightly touched the body feathers with the bill, when near their mate. On one occasion a female *E. calandra* was preening normally when a male suddenly landed by her. She began a courtship wing vibration, and her bill ceased to touch the feathers as she preened.

Very similar imperfect preening movements in which the bill did not quite touch the part of the body over which it was passed occurred as a part of "relevant" preening in nestlings of these species at about six days of age.

E. schoeniclus occasionally put the head down to almost between the legs as they approached a model of which they were afraid. This movement, which suggested an attempt to preen the belly, also occurred in *E. calandra* in fear, and in certain Carduelines (Hinde, 1955).

B. Pecking at Feet and Leg Ring

A caged male *E. schoeniclus* pecked quite normally at its toes or leg ring, in very brief pauses between hops or other movements, whilst it followed its female. A male *E. tahapisi goslingi* often behaved very similarly as it retreated after being threatened off by its female, and a female *E. bruniceps* occasionally did so immediately after being attacked by its male. Here irrelevant pecks were aimed at a definite source of irritation. Once a male *E. citrinella* which had been giving imperfect preening near his mate, began pecking so vigorously at his foot that he suddenly stood on one leg and withdrew the foot, apparently in pain.

C. Feather-settling

(1) *General.* Male *E. citrinella* sometimes gave feather-settling movements after a bill-raised sexual display (Andrew, in press) or after carrying nest material near the female. Occasionally the movements included both phases of wing vibration. They were also given after soliciting, and mild alarm. In the female *E. schoeniclus* they followed distraction displays and solicitings, and in the male, copulation attempts. Male *Calcarius lapponicus* and *Emberiza bruniceps* occasionally gave them after courtship displays.

E. calandra sometimes feather-settled after soliciting, or cooling responses given in fear. However 20/35 cases of irrelevant feather-settling in the field, were given by a male or female on meeting the mate after a period of separation. At some of these meetings the male or female gave first a low intensity courtship wing vibration which merged into the wing vibration of feather-settling. The male sometimes showed other sexual components and certainly often had a tendency to behave sexually. The wing vibration of the feather-settling was unusually marked, and may be regarded as "compromise behaviour" (Andrew, 1956), since it expressed both the tendency to feather-settle, and the sexual tendency.

When the irrelevant feather-settlings of *E. citrinella* were analysed, it was found that 23/36 occurred at the change from one type of activity to another. A feather-settling at the end of a bill-raised run, for example, might be followed by material carrying. An analysis of comparable cases in *E. calandra* showed the same for 13/23. Irrelevant feather-settling movements thus appear to occur when two conflicting tendencies are present, but neither are strong.

(2) *Feather-settling given by the female after copulation.* Female *E. citrinella* feather-settled after more than half of all their copulations; so, commonly, did female *E. hortulana*, *E. cirlus* and *E. calandra*. Unlike normal feather-settlings, the movement consisted of marked wing vibration of either phase with other components only weakly given. Female *E. citrinella* occasionally gave such a feather-settling between attempts to mount a soliciting male.

An important cause of this behaviour is probably the disarrangement of the primaries by the male's claws. However, feather-settlings occasionally occurred even though the male did not land. The marked wing vibration may also express a tendency to solicit. This would explain why, although a feather-settling wing vibration, it is so rarely divided into two phases.

D. Other Toilet Behaviour

E. citrinella (and also *E. schoeniclus* and *E. hortulana*) often wiped the bill in reproductive fighting, usually in pauses between lowering the bill or swinging the body, but occasionally whilst the bill was held lowered. Possibly it is the resemblance in form between bill-wiping and bill lowering that makes the former common in reproductive fighting. Usually the bill was wiped once on one or both sides; but occasionally the wiping was more persistent. Both male and female *E. citrinella* occasionally wiped the bill after copulation attempts. Once, a female wiped her bill very intensely and persistently whilst perched near two fighting males. Male *E. calandra* occasionally wiped the bill after an attack by a rival.

Two hand-reared *E. citrinella* occasionally stretched immediately after attacking another bird.

Several types of toilet behaviour may be given together irrelevantly. A female may bill wipe as well as feather-settle after copulation, or *E. calandra* may preen and bill-wipe when it meets its mate.

6. The Causes of Irrelevant Toilet Behaviour

Armstrong (1950) and Tinbergen (1952) noted that peripheral stimuli may decide which displacement activity is given, as is obvious in the pecking at leg rings described above. Andrew (1956) suggested that much irrelevant behaviour depends entirely on the same peripheral stimuli as cause its relevant occurrences (e.g. cooling responses in fear). This may be true of irrelevant toilet behaviour.

The peripheral stimuli for most types of toilet behaviour are fairly continuously present, and probably cause them to be given when other motivations are weak (above). The presence of appropriate stimuli is not in itself sufficient to explain the occurrences of toilet behaviour when other tendencies are strong. Feather-settling tends to occur at the change from one activity to another. At such moments of change the tendencies to give the two activities cannot be overtly expressed, and this may be why feather-settling can occur (caused in the same way as in its relevant occurrences).

Similarly, a toilet behaviour pattern may be given in conflict situations because a weak

tendency to give it can be overtly expressed at moments when two strong tendencies to give responses incompatible with each other are balanced. Morris (1954) notes that some individual idiosyncrasies are the same in both the irrelevant, and the normal bill-wiping of *Poephila guttata*, which confirms that their causation may be similar.

Foot pecking and bill-wiping were given on two occasions more vigorously in their irrelevant than in their normal occurrences (above). This does not necessarily mean that their causation is not similar in both. Hinde (1954) quotes a number of experiments which show that the intensity with which a behaviour pattern is given is sometimes increased by the arousing of another tendency.

Other examples of apparently irrelevant behaviour in the Buntings are not to be explained in this way, but appear instead to depend on central factors, which at first are not obvious. Male Buntings, for instance, often carry nest material during courtship; however, sexual and nest building responses are so generally associated in time, at low intensities, that they clearly share central causal factors. In addition, the bill-lowering of boundary disputes between male *Emberiza*, which Tinbergen (1939) suggests to be displacement feeding in the related *Plectrophenax nivalis*, may be homologous with movements of collecting nest material. If so, it is probably caused, like the sexual responses which occur during fighting between rival males, by a rival male having many features in common with a strange female (Andrew, in press).

Summary

The toilet behaviour patterns of *Emberiza* spp. are described. The peripheral stimuli important in their causation include foreign material on the feathers, bill or legs, disarray of the feathers, irritation in the respiratory passages, and a rise in the air temperature. Cases in which toilet behaviour is not caused in a general reflex-like way by peripheral stimuli are discussed. The general association together of toilet behaviour patterns is related to the fairly continuous presence of the appropriate peripheral stimuli, so that all the patterns tend to be given whenever other motivations are weak.

The irrelevant occurrences of toilet behaviour are described. Feather-settling tends to occur at the change from one type of activity to another. Possibly when incompatible tendencies are so equally balanced that they cannot be overtly expressed, a weak tendency to give a toilet behaviour pattern can result in its being given irrelevantly. The irrelevant carrying of nest material in courtship depends chiefly on central causal factors.

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NOTES ON THE BIOLOGY OF *Leiurus quinquestriatus* (H. & E. 1829) *(Scorpiones, Buthidae)*

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Vachon (1952) has summarised the scanty literature on the biology of scorpions, and pointed out that their courtship behaviour has been adequately described in the case of but a single species, *Buthus occitanus* (Amoreux, 1789). Very little is known of the biology of the group, and there are no records concerning the biology of *Leiurus quinquestriatus*.

Hemprich and Ehrenberg regarded *Leiurus* as a sub-genus of *Androctonus* H. & E. 1829 (Vachon, 1952). Four of the five species of *Leiurus* have since been assigned to other genera, and recently Vachon (1952) has elevated it to generic rank, with the single complex species *quinquestriatus* divided into two sub-species, *quinquestriatus* (H. & E.) and *hebraeus* Birula. The range of the former extends across North Africa, the southern boundary of its distribution lying within the Sudan. It is, however, one of the commonest species in Khartoum.

Courtship Behaviour

At 10.30 hrs., on 19th August, 1954, a freshly caught male *L. quinquestriatus* was introduced into a large glass container in which was a well fed female of the same species, which had been kept there in isolation for the previous three weeks. The bottom of the container was covered with a layer of sand three inches deep.

After half an hour of complete immobility, the male began to walk around the edge of the container, until it met the female head on. Here it stopped, and after a few testing movements of its pedipalps it quite suddenly gripped the pedipalps of the female in its own, the chelae of the male enclosing both joints of the closed chelae of the female. The male next proceeded to walk backwards round the container, the female, being held by the pedipalps, following. After three minutes of this procedure the male stopped and became immobile once more. The female then took the initiative by making, every one or two minutes, short forward movements accompanied by slight relative forward movements of the telson. The trochanters of the female's pedipalps came into contact with the corresponding joints of the male's for a few seconds, and the chelicerae of the two individuals almost touched. These movements continued, with short periods of inactivity, for twenty minutes, when the male again began leading the female, occasionally stopping to make the contacts just described, the female responding in like manner. At one time the female appeared to be pulling away from the male, which responded by bending its pedipalps, thus drawing the female towards it until their trochanters touched. The "promenade à deux" continued for forty-five minutes, and was followed by another half-hour period of inactivity with the two scorpions facing each other, the pedipalps of the male all the while gripping those of the female. The male next began to bend one pedipalp at a time, straightening somewhat the corresponding pedipalp of the female. By this alternate bending of the pedipalps the female was drawn forward slightly. The male then became very active, with the metasoma tightly curled vertically, and during the next fifteen minutes repeated all the above movements. Three hours after courtship began, all activity stopped for the rest of the day, but the male did not relax its pedipalp grip.

The next morning both scorpions were lying in a burrow, and no further activity was seen during the day. The two scorpions lived together until 25th September, when the male died. Both scorpions were observed to be active above the surface at night during this period.

On two other occasions courtship was essentially the same, and again the actual copulation was not observed. In these two cases, however, the male was killed and almost wholly eaten by the female during the night following the courtship.

Gestation Period

On 22nd November, 1953, courtship was observed, the male being eaten. The female genital opening was devoid of a spermatocleutrum before the introduction of the male, but after its death a spermatocleutrum was seen. The female gave birth on 26th April, 1954, having since been kept in isolation; the gestation period was thus 155 days.

Number of Offspring

Three different individuals have given birth in the laboratory, the numbers of their offspring being 82, 42 and 77. Dissection of pregnant females has revealed the following numbers of embryos; 58, 49, 63, 41, 56, 50.

Copulation Period

The three laboratory births mentioned above occurred in the months of April, September and October. With a five month period of gestation the dates of copulation would be November, April and May, respectively. November being in the winter and April and May in the dry part of summer before the rain. It thus seems likely that in the Sudan this species has no definite mating season.

Burrowing Activity

When kept in the laboratory, *L.quinquestriatus* has always made a shallow burrow in the sand, with two, three or four exits. The animals remain about three centimetres below the surface during the day, emerging at night. There seems to be no previous record of such a habit for this species. The burrowing is done by the first, second and third pairs of walking legs, which fling the sand backwards by rapid flicking movements, while the scorpion is supported by the fourth pair. The pile of sand thus formed is periodically dispersed by a number of horizontal sweeps of the tail posteriorly, accompanied by a straightening of the metasoma.

Remarks

The courtship behaviour of *L. quinquestriatus* is generally similar to that of *Buthus occitanus* so graphically described by Fabre (1907), except for the absence, on the three occasions observed, of the "arbre droit." It would seem that this is not invariably a preliminary phase in the courtship of *L. quinquestriatus*. The "promenade à deux," including the alternate pedipalp movement and occasional trochanter touching, is markedly similar in the two species.

Vachon points out that there is some disagreement as to the length of gestation in *B. occitanus*, but three of the four observers cited give periods of 11 months or more. The relatively short period indicated for *L. quinquestriatus* may be an effect of temperature.

The number of offspring, 41-82, is similar to the numbers recorded for other species.

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A STUDY OF THE STIMULI WHICH RELEASE THE FOOD BEGGING AND OFFERING RESPONSES OF WORKER HONEYBEES

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Introduction

Frequent transmission of food occurs between the workers of a honeybee colony (Nixon & Ribbands, 1952; Istomina-Tzvetkova, 1953). The possible evolution of this behaviour is discussed by Free (1955). In the present work a study has been made of the stimuli to which a bee reacts when it either begs food from, or offers food to, another bee.

The Stimuli which Release the Begging Response of a Hungry Bee

When a worker bee solicits food it extends its proboscis and thrusts the tip towards the mouth-parts of another bee. If the soliciting bee is successful the other bee responds by regurgitating food. The antennae of each bee are continually in motion during feeding and are constantly contacting those of the other and undoubtedly have an orientating function (Fig. 2).

The Scent of the Head

Preliminary observations had indicated that hungry bees readily beg for food from the excised heads of other bees. In the first experiments the part that the scent of a head played in releasing the begging response of a hungry bee was investigated.

The arena used in the experiment is shown in Figure 2. It consists of a block of wood with a central hole 3 in. in diameter, covered on top by a sheet of glass. A cork pushed up to within ½-in. of the glass roof formed the floor of the arena. The excised heads of 16 bees were mounted on pins in the arena so that they were at the "normal" height and position relative to its floor (Fig. 1). Eight of these heads which were from recently killed bees were arranged alternately in a circle with 8 other heads that had been boiled in potassium hydroxide and washed with water to remove any scent.

Starved bees were placed, one at a time, in the centre of the arena and the number of times they made antennal contact with, or begged from, each head was recorded. A bee was removed from the arena after 30 minutes or as soon as she had made 20 such responses.

The starved bees examined with their antennae the heads of recently dead bees a total of 112 times and subsequently begged from them 91 times. Although they examined the heads that had been boiled in potassium hydroxide 88 times they only begged from them 3 times (degree of significance $P < 0.001$).

In a similar experiment the heads of recently dead bees were rubbed against heads which had been treated with potassium hydroxide in an attempt to transfer any scent present on the former to the latter. Although the hungry bee still begged more frequently from the heads the newly killed bees (47 : 15 begging reactions), the heads that had been boiled in potassium hydroxide were significantly more attractive than in the previous experiment ($P < 0.001$).

It was apparent from these experiments that the scent of a head is an important stimulus in releasing begging behaviour.

In a further experiment 8 heads of bees which belonged to the same colony as the starved bees, and 8 heads of bees taken from another colony, were alternated in a circle. The starved bees made antennal contact with heads of bees from their own colony 101 times and with heads of bees of the other colony 99 times, but they subsequently begged from the former on 89 occasions compared with the 53 occasions on which they begged from the latter (degree of significance $P < 0.001$).

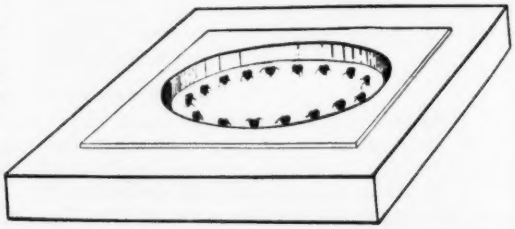

Fig 1. The arena used during the experiments showing 16 heads arranged in a circle

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Fig. 2. Food transmission between two worker honeybees. The bee on the left is giving food to the bee on the right

Not only, therefore, does the scent of any bee's head release the begging response of a hungry bee, but heads which emanate the same colony odour (Kalmus & Ribbands, 1951) as that of the begging bees possess a greater releasing value.

The Colour of the Head

The clypeus, frons and antennae of 8 heads were painted white and those of another 8 heads were painted black. The black and white heads were then alternated in a circle in the arena. Starving bees introduced to the arena examined the white heads 107 times and begged from them 69 times, and examined the black heads 93 times and begged from them 58 times (no significant difference).

Models of heads made of cotton wool were used in another experiment and were painted black or white and rubbed with the heads of bees to give them the correct odour. The black models were examined 59 times and begged from 12 times, and the white heads were examined 41 times and begged from 10 times (no significant difference).

The normal black colour of a bee's head does not, therefore, appear to act as a stimulus which releases the begging response.

The Form of the Head

It was thought that the triangular shape of a bee's head might direct the begging response towards its mouth-parts. A circle of heads was, therefore, arranged in the arena so that each alternate one was inverted. When starving bees were placed in the arena they examined those heads that were the "right way up" and those that were the "wrong way up" an approximately equal number of times (53 : 47) but they subsequently begged from the former significantly more often (49 : 35) (degree of signifiance $P<0.05$). The reason for this will become apparent later. In every case, however, the begging bees directed their tongues at those parts of the heads nearest to the floor of the arena, so that they, in effect, begged from the tops of those heads which were inverted.

In a further experiment 8 heads were pinned flat on the floor of the arena with their faces uppermost. Hungry bees begged from these heads on 50 occasions. On 21 occasions they begged from the sides of the heads, on 14 occasions from the tops, on 8 from the bases (in the region of the mouth-parts) and on 7 from the fronts of the heads. Therefore, although they preferred to beg from the edges of the heads, the mouth-parts received no special attention.

Observations were made to determine whether the front of an upright head released more begging responses than its back. Eight heads were pinned in a circle and arranged so they alternately faced inwards and outwards. Hungry bees begged from the fronts of the heads 141 times and from their backs only 59 times (degree of significance $P<0.001$). The striking difference between the front and back of a bee's head is the projection of antennae from the front part, so the above experiment was repeated but this time the antennae were removed. There was no significant difference in the number of times that the bees begged from the fronts or backs of the heads (102 : 98).

It appeared, therefore, that hungry bees more often begged from the fronts of heads than from their backs simply because the former possessed antennae, and that the antennae were important stimuli in releasing the begging reation.

When 16 heads were arranged in a circle and the antennae from each alternate one were removed, hungry bees begged 134 times from heads with antennae but only 66 times from heads without antennae. (degree of significance $P<0.001$). In a similar experiment, conducted in red light, in which the bees were unable to see, the starved bees begged 147 times from the heads with antennae and 53 times from the heads without ($P<0.001$). The antennae must, therefore, act as contact stimuli.

Experiments were made to determine whether "model" antennae would elicit similar responses to those elicited by real antennae. Antennaless heads were arranged in a circle so that they alternately faced inwards and outwards and 2 small pieces of wire of approximately the same diameter and length as antennae were fixed to each. The presence of these "model" antennae had a significant effect ($P<0.001$) in releasing the begging response (Table I).

When the releasing function of the antennae had been established, it became apparent that in the above experiment in which heads were alternately arranged the right way up and upside down, the former probably received more begging responses because their antennae were correctly orientated to those of the hungry bees.

Table I. The Effect of Model Antennae on Releasing Begging Responses

	No. of times hungry bees begged from front of head	No. of times hungry bees begged from back of head
"Model" antennae fixed to front of head	62	38
"Model" antennae fixed to back of head	82	118

Table II. The Number of Times Hungry Bees Begged from the Different Parts of Dead Bees

	No. of times begged from head	No. of times begged from thorax	No. of times begged from abdomen
Experiment 1. Heads of dead bees with antennae intact	139	20	41
Experiment 2. Heads of dead bees with antennae removed	41	28	31

Table III. A Comparison of the Releasing Value of Excised Heads and Abdomens

	No. of times starving bees begged from heads	No. of times starving bees begged from abdomens
Experiment 1. Heads with antennae ..	69	31
Experiment 2. Heads without antennae ..	109	91

The Head in Relation to the Remainder of the Body

Attempts were next made to determine why a bee normally begs from the head of another bee rather than from some other part of its anatomy.*

The experiments were similar to those already described except that entire bees were fastened to the floor of the arena and arranged in a circle so that they alternately faced in opposite directions. The results are given in Table II.

Although the hungry bees begged more frequently from the heads of dead bees than from other parts of their bodies, the responses to the heads were greatly reduced after their antennae had been removed and, under these circumstances, an abdomen and a head had a similar releasing value. A direct comparison of the releasing value of abdomens and heads was made by arranging excised abdomens (with their posterior ends upwards) and excised heads alternately in a circle (Table III). When the heads were without antennae the abdomens and heads released a similar number of reactions.

In a similar experiment in which the number of reactions to excised abdomens and thoraces was recorded, the former were begged from 72 times and the latter only 28 times ($P < 0.001$). A further demonstration of the greater attractiveness of the abdomen in comparison with the thorax was shown in another experiment. Eight headless bodies were placed in the arena and one head was pinned in the normal position in front of the prothorax and another at the tip of the abdomen of each. Hungry bees begged significantly more ($P < 0.01$) from those heads that were attached to the abdomens (120 times) than from those heads in the normal position (80 times).

The Effect of Movement

A final experiment was made to determine whether the movement of one bee acted as a stimulus in releasing the begging responses of another. Four dead bees and 4 live bees were

*A very hungry bee will beg from any part of another bee's body.

fastened in the arena. The antennae and legs of the live bees were in almost constant motion and the rest of their bodies was also capable of limited movement. Hungry bees begged from the live bees 212 times and from the dead bees 188 times. Movement therefore appeared to exert little or no effect in eliciting the begging responses.

The Stimuli which Release the Offering Response of a Bee

A bee which offers food to another opens its mandibles, raises the proximal part of its proboscis and often regurgitates a drop of fluid.

Bees which had been fed with sugar syrup were placed in a small arena. When one was seen to offer food it was removed and placed in the "experimental" arena and observed for 30 minutes or until it had offered food 20 times. It was then replaced by another bee which had been observed offering food.

The first experiment was made to determine whether offering, like begging, is an orientated reaction. Recently killed bees were fastened to the floor of the arena and records made of the parts of their bodies towards which the heads of the fully fed bees were directed when they offered them food. The heads of the dead bees received 132 offers of food, their thoraces 21, and their abdomens 47. Thus it is apparent that offering behaviour, like begging behaviour, is orientated primarily towards the head of a possible recipient.

In the next experiment 8 bees, 4 of which had recently been killed and 4 of which were alive and capable of limited movement, were fastened to the floor of the arena. The well-fed bees offered food to the live bees 151 times but only 49 times to the dead bees (degree of significance $P<0.001$). Therefore, although movement does not appear to be one of the stimuli that releases the begging response, it does play a part in releasing the offering response.

When a well-fed bee offered food to a bee fastened in the arena, the antennae of the offering bee often contacted those of the potential recipient. It was decided to determine whether the release of an offering response, like that of a begging response, was influenced by the presence of antennae. Sixteen heads were pinned in a circle in the arena and the antennae were removed from each alternate one. Well-fed bees offered significantly more ($P<0.01$) to heads with antennae (120 times) than to heads without (80 times).

The scent of a bee's head was also important in releasing the offering response, and, in a similar experiment to one described above, well-fed bees offered food to scentless heads (i.e. heads which had been boiled in potassium hydroxide and subsequently well washed with water) 17 times compared with the 83 times that they offered food to the heads of freshly killed bees (degree of significance ($P<0.001$).

Well-fed bees exhibited marked differences in their behaviour towards the heads of bees of their own colony and to those of heads of other colonies. Their behaviour on 200 occasions on which they were observed to make antennal contact with the heads in the arena are given in Table IV.

The Functions of Antennae in Reciprocal Feeding

The function of the antennae in the transmission of food from one bee to another was further studied by observing the behaviour of live bees whose antennae had been amputated.

Eight hungry bees were placed in a small arena; 2 of these bees had both antennae intact, 2 had one antenna entirely removed, 2 had the flagellae of both antennae removed, and 2 had both antennae entirely removed. On each occasion that one of these bees begged from another its identity and that of the bee from which it begged were recorded. Each experiment was continued until 50 such observations had been made. The hungry bees were then replaced

Table IV. The Reactions of Fully Fed Bees to Heads Belonging to Their Own and Another Colony

	No. of reactions to heads of bees of their own colony.	No. of reactions to heads of bees of another colony.
Ignored	13	8
Offered food	68	51
Recoiled	2	9
Buzzed violently	2	21
Bit	2	20
Attempted to sting	0	4

Table V. The Number of Times Bees with Various Proportions of their Antennae Removed Begged for Food and were Begged from by Other Hungry Bees

	Number of times food begged *from* bees with:				
	a Both antennae intact	*b* One antenna removed	*c* Flagellae of both antennae removed	*d* Both antennae removed	Total
No. of times food begged *by* bees with:					
a Both antennae intact ..	110	130	57	44	341
b One antenna removed ..	99	19	21	11	150
c Flagelle of both antennae removed	3	3	0	0	6
d Both antennae removed	1	1	0	1	3
Total	213	153	78	56	

with 8 others that had been similarly treated until 10 experiments had been completed, giving a total of 500 observations. The results are shown in Table V.

It is clear that those individuals which had both their antennae completely or partially removed did not beg for food to any extent and were not begged from as much as those bees who had one or both antennae intact. Bees with one antenna only begged less than half as much as normal bees and did so mostly from normal bees.

In a similar series of five experiments, 8 well-fed bees were placed in the arena. The results are given in Table VI.

Bees with both antennae intact were most frequently offered food whilst bees with no antennae were least often offered food. Although bees with both antennae partially or completely amputated did not offer food as often as bees with one or both antennae intact, they did do so on a considerable number of occasions. Therefore, it appears that whereas the possession of intact antennae is essential for a bee to be able

Table VI. The Number of Times Bees with Various Proportions of their Antennae Removed were Offered Food by and Offered Food to Other Well-fed Bees

	Number of times food was offered *to* bees with :				
	a Both antennae intact	*b* One antenna removed	*c* Flagellae of both antennae removed	*d* Both antennae removed	Total
No. times food offered *by* bees with:					
a Both antennae intact ..	13	26	16	14	69
b One antenna removed ..	44	21	10	5	80
c Flagellae of both antennae removed	26	17	7	8	58
d Both antennae removed ..	18	11	12	2	43
Total	101	75	45	29	

Table VII. Number of Bees Dead after Twenty-four Hours

	Bees with both antennae amputated	Bees with one antenna amputated	Bees with both antennae intact
Cage 1. Supplied with feeder ..	18	0	1
Cage 2. Not supplied with feeder ..	18	15	6

to beg for food, it is unnecessary for a bee to be able to offer food. This difference is probably explained by the fact that whereas movement plays no part in eliciting the begging response, it is of considerable importance in releasing the offering response. The above data would seem to indicate that movement itself is sufficient to release the offering response.

In order to obtain quantitative data of the value of antennae to a bee seeking food, the following experiment was carried out. Eighteen bees from which both antenna had been removed, 18 from which one antenna had been removed, and 36 normal bees were placed in each of 2 cages. A feeder containing sugar syrup was given to bees in one of the cages but the bees in the other cage were not provided with food. After twenty-four hours the number of dead bees in each cage were counted (Table VII).

When ample food was available (Cage 1) bees with one antenna survived as well as those with both antennae. However, when food was scarce (Cage 2) the death rate of bees with one antenna was greater, thus indicating that they could not obtain food as effectively as normal bees.

The Behaviour of Newly Emerged Bees

Numerous young bees, all of whom had emerged in the absence of older bees, were seen to feed one another and both to offer and beg food when less than twenty-four hours old. The behaviour patterns associated with food transmission are therefore innate.

The first attempts of 33 young bees to obtain food were observed. They were taken from their comb immediately after emergence and placed, one at a time, in a small arena containing 5 older bees. In most cases they attempted to obtain food within a few minutes. In one case a bee which had not completely emerged from its cell begged from a passing worker, and in another a bee with only its head out of its cell was offered food. The begging responses of newly emerged bees seemed to lack the precision and co-ordination of older bees, and in many cases they begged from the thoraces and abdomens of older bees. Even when a recently emerged bee orientated its proboscis toward the head of another bee it often failed to contact the mouth-parts of the other bee. However, many of the newly emerged bees managed to obtain food during the first 30 minutes of their adult lives.

There is little possibility of bees dying by starvation because of their inability to obtain food shortly after emergence, as the length of life of 20 bees isolated on emergence and not provided with any food ranged from 20 hours 38 minutes to 26 hours 50 minutes. In any case newly emerged bees may feed themselves from honey in a cell, rather than obtain food from another worker.

Bees a few days old which had been isolated since emergence and then introduced to other live bees appeared to beg and to offer food perfectly at their first attempts. In order to obtain objective data, bees of 3-5 days old, which had been isolated from emergence were placed in an arena in which there were 8 dead bees and records were taken of the parts of the dead bees' bodies which the isolated bees approached when they offered or begged food. The results are given in Table VIII and indicate that these isolated individuals orientated their

Table VIII. The Parts of Dead Bees' Bodies to which Unconditioned Bees Reacted when Offering or Begging Food

	Head	Thorax	Abdomen
No. of times food begged from:	158	15	42
No. of times food offered to:	138	20	47

responses towards the heads of the dead bees as frequently as bees which had lived in a normal colony.

Discussion and Conclusions

In common with other innate reactions (Tinbergen, 1951) the begging and offering responses of bees are released by only a few out of a number of possible stimuli. The scent of a head and the presence of antennae are important stimuli, whilst the shape and colour of the head appear to be irrevelant. Movement plays no part in releasing begging behaviour but does so in releasing offering behaviour. Whereas some of the responses studied in other animals are released by stimuli which appear to serve no other purpose (e.g. the mew call of the adult herring gull and the red patch on its bill tip (Tinbergen, 1951)), none of the stimuli which release the begging and offering behaviour of a bee appear to be developed solely for this purpose

Scent is probably the most important releaser and heads which are placed at the ends of the abdomens of dead bees are responded to more frequently than they are when in their normal position. This is probably due to the fact that under these circumstances the attraction of these heads is combined with the scent produced by the Nassanoff glands which are situated near the tips of the abdomens and which are by themselves strongly attractive to bees (Free & Butler, 1955).

An additional important factor in releasing begging behaviour is recognition of the odour of a head as belonging to a companion from the same colony. Well-fed bees will often attack the heads of bees from other colonies. Butler & Free (1952), Ribbands (1954), and Free (1954) have shown that guard bees recognise intruders by their scent and it now seems likely that a guard bee is able to distinguish between a member of her own colony and an intruder from another colony by the scent of its head alone.

Istomina-Tzvetkova (1953) and Free (1956) found that bees of one day old both gave and received food, although they received food more often than they gave it, and in the present work newly emerged bees, which were segregated from older bees, were found to feed one another when less than a day old. Although the begging and offering responses of bees improve in precision with age, learning appears to play little part in the process. This has been found to be true of the maturation of behaviour patterns of certain birds (Thorpe, 1951).

Summary

1. A study has been made of the stimuli to which worker bees respond when they offer food to or beg food from other workers.

2. Offering and begging behaviour is directed more to the head than to other parts of a bee's body, and excised heads alone are sufficient to release both responses.

3. The scent of a head is an important stimulus, and heads possess a greater releasing value if taken from bees belonging to the same colony as that of the offering and begging bees.

4. The colour and shape of the heads is of little or no importance and hungry bees beg from the lowest part of a head irrespective of its orientation.

5. The antennae on a head provide a contact stimulus with a releasing function. It is possible to simulate their effect by the use of "model" antennae.

6. Bees whose antennae had been removed were able to offer food but not to beg for it. The presence of both antennae is necessary for a bee to beg food with the maximum efficiency.

7. Whereas movement appears to play no part in releasing the begging response, it is of significance in releasing the offering response.

8. Both begging and offering are innate reactions and improve in precision with age, independently of conditioning.

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A STUDY OF DIFFERENCES IN THE SEX DRIVE OF COCKERELS

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A number of workers using different observation periods and methods have shown that cocks mate at different rates (Penquite, Craft & Thomson, 1930; Skard, 1937; Parker, McKenzie & Kempster, 1942; Guhl, Collias & Allee, 1945; Guhl, 1951 and Wood-Gush, 1954). As yet, however, no attempt has been made to correlate these differences in libido with fertility records or semen production. Furthermore, no investigation into the possible causes of these differences has been attempted with fowls, although recently Craig, Casida & Chapman (1954) have attempted such an investigation in a population of rats. In the present work it is shown that the differences in the libido of 30 cockerels appear to have a genetic basis and the relationship between their semen production and sexual rankings is examined. A number of males consisting of both high and low ranking ones in the sexual hierarchy were also tested for fertility. Finally, it is shown that there is a highly significant negative correlation between a male's sexual ranking and his comb conformation.

Material and Methods

Observations of mating frequency were made on each of 30 cockerels—15 pairs of full-sibs and 6 sets of half-sibs—from a sub-unit of the Edinburgh flock of Brown Leghorns which was derived for experimental purposes from the original Line B, or control line. Since this separation in 1952 the sub-unit has been subject to some selection for winter egg production, but inbreeding over and above the then prevailing coefficient of 25 per cent. has been avoided. The results thus correspond to such as may be found in an average production-bred closed flock, the extent of genetic variation being presumably less than that which may be demonstrable between different breeds, strains or inbred lines.

The cockerels, who had been reared together were all aged between 6 and 7 months at the start of the experiment. When not in use, they were caged in pairs at random (i.e. not related pairs), and immediately after use were returned to the cages.

During the month prior to the start of the experiment, each cockerel was put into a pen of laying pullets for 48 hours and this constituted his first sexual experience. Again, two days prior to a cockerel's first period under observation, he was placed in a pen of laying pullets and removed at 10 a.m. on the day when he was to be observed, and caged singly. In these operations, great care was taken to ensure they were placed in pens containing comparable numbers of receptive females, thus ensuring that their sexual experiences would be uniform.

Two observation pens were employed, and each cockerel was observed twice in each, for one hour at a time. The order in which cockerels were taken for the first observation was randomized. Thereafter the intervals between successive observations on each cockerel were kept moderately constant. At the same time, however, it was arranged so that no bird ever succeeded the same bird twice—his predecessor in the pen the previous afternoon was always a different bird. Only one observation per day was made on a pen and this was done between 16.00 and 17.00 hours, for the maximum number of copulations takes place in the late afternoon (Upp, 1928; Skard, 1937; Parker, McKenzie & Kempster, 1940; Long & Godfrey, 1952). The observations commenced in late November, 1954, and ceased in the first week of March, 1955. During this period, all birds were housed inside and kept under artificial light so as to simulate a constant day length. The number of hens in the 2 pens were 14 and 11, and all remained in lay during the period of the experiment. Before release into a pen, the condition of a cockerel was noted and if he appeared to be "off-colour" his observation period was postponed. When semen was collected, care was taken not to use any cockerel who was to be observed shortly.

When copulating, the cock mounts the hen, grabbing her by the back of the neck, treads her for a few seconds then brings his cloaca into contact with hers. Incomplete matings are common; the cock may just mount the hen or he may mount and tread her without cloacal contact. During the observation period all

*The first author is responsible for the behavioural observations in this work, and the second author for the statistical analysis.

attempted and completed matings were recorded, and were scored as follows: (1) mountings, (2) treadings, and (3) successful treadings, i.e. mounting, treading and cloacal contact. It was also noted whether any of these three types were male initiated, female initiated or mutually initiated. In addition, in Pen A the displays of the cockerel and his general behaviour were also noted so that a fairly comprehensive idea of his behaviour was obtainable from the records. The observer in each pen was hidden and the method of release of the cockerel was standardised as far as possible. Throughout the experiment, all birds were housed indoors.

Results

1. Mating Behaviour

Firstly, the data were analysed with each type of mating given equal weight so that the individual score for a cockerel represented his total number of matings within an observational period. A marked variation of the individual figures of mating frequency between zero and 25 per hour was found. Even casual observation of the results was sufficient to indicate that mounting frequency was a markedly individual characteristic and also that marked family differences were present. As an example, eight observations of zero were found for two full brothers, whilst the observations for two brothers from another sire family were

(*a*)	7	7	1	7
(*b*)	8	9	8	13

Likewise, cases of marked variation between full-sibs were readily observable, a typical set of observations for two brothers being

(*a*)	2	3	4	5
(*b*)	12	9	11	9

Undue weight is not to be placed on such isolated examples; they are given merely as a background to the analyses of variance detailed under Biometrical Methods (B.M. 1) and to give a visual picture of the type of variation present.

To allow for a difference between the means and variances of the two pens and to illustrate the high degree of correspondence between repeated observations an analysis was carried out separately for each pen. In both cases variation between the 30 individual cockerels is highly significant. Furthermore in both cases the significance of variation, as in the above cases, is derived from two sources—variation between full brothers and variation between cockerels from different sire families. That genetic differences are present is indicated by the latter though some doubt is raised by the insignificance, in both pens, of contribution by the female parent—i.e. within sire families the variation between dam families is insignificant. Subject to further investigation one pointer is suggested. Both male and female parents were selected on family records for egg production with, in the case of females, additional selection on individual merit. The choice of individual unscored males from superior families as opposed to groups of highest producing females in such families, may, so far as production is concerned, have lessened the potential genetic variability of female parents; a correlation between sexual activity of cockerels and genotypes of their parents for egg production would give results as above. Data on this aspect of the problem are as yet incomplete, but the existence of a sampling effect in the above or similar sense would appear more feasible than the existence of a particular genetic mechanism such as patroclinous inheritance.

As already noted, the correspondence between replications is high; and illustrations of rankings of particular groupings in each pen may be given to further clarify the analysis of variance summaries. For the six-sire families the mean mating frequencies are

	Pen A	Pen B	*n*
1	11.00	6.38	2
2	6.50	7.25	6
3	6.42	5.42	6
4	5.58	3.50	4
5	3.38	3.38	4
6	3.25	2.44	8

where *n* is the number of cockerels per family. Apart from an inversion in the case of the first two families (one family being represented by only two cockerels) the ranking of families is the same in both cases. Further good agreement is observed in the ranking of brothers within each dam family. Table I gives the total score of each cockerel in each pen. The two entries in each sub-group are the scores for two brothers, the order of entry being the same for the two pens. A + sign indicates agreement between rankings, a — sign, reversal, and it will be observed that only in 3 families out of 15 is there a change of rank. The sire family classification and extent of variation between sire families may also be observed from this table.

Table I. Mating Frequencies of Individual Cockerels from Fifteen Families in Each of Two Pens

Sire family	Dam family	Pen A		Pen B		
1	1	5	21	9	20	+
2	2	5	15	8	9	+
	3	8	24	11	17	+
	4	15	10	9	11	—
3	5	13	9	3	8	—
	6	15	20	2	17	+
	7	4	6	3	9	+
4	8	4	10	10	5	—
	9	9	4	6	6	?
5	10	38	19	12	10	+
	11	14	17	8	21	+
6	12	9	14	8	14	+
	13	0	0	0	0	
	14	2	11	2	4	+
	15	11	5	6	5	+

Finally, for the 15 families in Table I there is a correlation of 0.70 (1 per cent. significance) between the total frequencies (sum of two brothers' values) in each pen. The tests of significance (B.M. 1) and similarity of results for the two pens thus leave little doubt of the reality of the observed differences. Furthermore, the differences between the sire families emphasise the genetic basis of the character.

It was mentioned earlier that the three types of matings—viz. mountings, treadings, and successful treadings—were also classified into male initiated, female initiated, and mutually initiated. It was argued that giving these various types of matings differential scores might further influence the variation between cockerels. For example, one successful treading might be followed by a temporary pause in the cockerel's courtship, while another male in an equal period of time might mount several hens several times without treading them. If all types of matings are given equal scores then the second cockerel will have the greater score, but there can be little doubt that the first cockerel has displayed a higher degree of sexual activity. Similarly, it might be argued that a cockerel forcibly mounting a female shows a higher degree of sexual activity than a cockerel who quietly mounts a crouching female, for the second cockerel is responding to a possibly greater stimulus. On the basis of these arguments five categories of mating were formulated and arbitrary scores were assigned to each in accordance with the degree to which they might be expected to reveal the sexual activity of the cockerel.

The classifications and scores assigned were

v	Successful treadings	5
u	Treadings	3
z	Mountings mutually initiated	2
y	Mountings male initiated	2
x	Mountings female initiated	1

Such scoring did not affect the previously given results in any way. For the 60 individual observations in Pen A the correlation between weighted and unweighted scores was 0.968, for the 30 cockerel totals in the same pen (each value the sum of two replications) the correlation was 0.975, for the 15 dam family totals 0.984, and for the 6 sire famliy means 0.992 (means being used because of unequal numbers of observations per sire). Likewise the ranking of sire means was the same in both cases whilst only 2 families out of 15 gave a reversed ranking of full brothers. Analyses of variance again gave results in accordance with the unweighted analyses.

Such a method of arbitrary scoring, whilst plausible on *a priori* grounds, does not, however, distinguish between the actual contributions which each type of mounting contributes towards the significance of individual and genetic variations. To this end the method of discriminatory analysis (Fisher, 1948, p. 285) was undertaken. Thus instead of taking the total mountings of a cockerel, $x + y + z + u + v$, as a criterion, the problem was to seek a linear function $L = b_1 x + b_2 y + \ldots b_5 v$ which, by giving a particular weight to each type of mating, would maximise the significance of variation between cockerels. However, the discriminant function calculated on an approximate basis in B.M. 2 showed virtually no advantage over the unweighted analysis regarding the relative amount of the total variance attributable to differences between cockerels. It is evident that no statistical significance can be attached to the deviations of the calculated weights from unity. In actual fact, such a

Table II. The Sexual Rank of Each Cockerel and the Assessment of its Semen Samples. Each sample was classified on the basis of volume, sperm density and morphology of the spermatozoa

Cock	Rank	1st Sample 15/12/54	2nd Sample 17/1/55	3rd Sample 14/2/55
4293	1	Good	Good	Average
4344	2	Poor	None	Poor
4341	2	Average	None	
4669	4	Average	Poor	Poor
4677	5	Average	Good	Good
4661	6	Average		
4334	7	Good	Good	
4330	8	Average	Good	
4692	8	Good	None	Average
4299	10	None	Poor	Poor
4951	11	None		Average
4014	12	Good		Average
4316	13	Average	Average	Poor
3996	13	Poor	Poor	None
4307	13	Good	Good	Good
4691	13	Average	Good	None
4032	13	Average	Average	Average
4035	18	Good	Good	Poor
4682	19	Poor	Average	Average
4308	19	Good	Poor	Good
4321	19	Average	None	Average
4698	19	None	Poor	Poor
4007	23	Good	Good	Poor
4041	23	Poor	None	Poor
4699	25	None	None	Average
4968	25	Poor	Average	Average
4022	27	Average	Poor	
4001	28	Good		Good
4295	29	Poor		Poor
4927	29	None	None	Poor

widely divergent function as $L = x + 2y + 2z + 3u + 5v$ gave correlations in the region of unity between weighted and unweighted scores, and it is evident that a wide range in scores will be without effect on the final analysis. The simplest, and a satisfactory method, noting that all variables contribute towards significance in the same direction, is to take the total frequency of all types of mating as the criterion of individual behaviour.

2. Semen Collection

Three collections of semen were made from the majority of cockerels, the first in December and the other two in January and February. Collection was by massage and no cockerel was employed if he was to be tested shortly or had been tested recently. Each sample was examined microscopically, its volume and density assessed, and the morphology of the spermatozoa examined. After this assessment each sample was classified as good, average or poor, and the results are shown in Table II. There appears to be little or no relationship between a cockerel's semen sample and his position in the sexual hierarchy. Furthermore, most cockerels are very variable in their yields. Similar intra-cock variability in volume and density has been reported previously (Parker, McKenzie & Kempster, 1942) and the possible causes of it will be discussed later.

3. Differences in Fertility

Unfortunately, it was impossible to test the fertility of all the cockerels under breeding pen conditions. However, the 5 worst and 5 best cockerels of the sexual hierarchy were divided into 5 pairs of good and poor performers. A pen of females was allotted to each pair and a fertility test was performed, allowing each member of a pair 48 hours in the pen. Since Penquite, Craft & Thompson (1930) had observed that their best cocks inseminated 8 females in a day (12 hours), it was estimated that the best cockerels in this experiment would be able to inseminate most of the laying females in their pens. The general fertility was poor, but this might have been due to a severe outbreak of feather picking earlier amongst the females, so that at the time of the tests the majority of them were "bare-back" and thus possibly unreceptive to the males. After the removal of a male, all eggs were collected over the next 15 days, set, and eventually candled. On the 9th June, 16 days later, the other member of the pair was then introduced into the pen. Despite the poor fertility the high ranking cockerel, with one exception, inseminated more females than its team-mate. The 5 high ranking cockerels inseminated a total of 17 females whilst only one low ranking male fertilised any eggs at all. In the exceptional case, the low ranking cockerel inseminated 3 hens as opposed to 2 inseminated by his team-mate. It must be stated that at the time of these tests all cockerels yielded semen samples that were judged to be adequate for insemination.

4. Correlations of Mating Activity and Comb Size

It was noted during the periods of observation that many of the sexually inactive cockerels possessed large floppy combs, and statistical analysis further substantiates the reality of this observation by showing the existence of correlation between comb size and frequency of mating.

Measurements of comb height and width were taken on each of 27 of the cockerels available at this stage of the experiment. Both measurements were negatively correlated with the total mating score for each cockerel (the sum of four observations), the appropriate coefficient being

Comb height and width	+ 0.7378
Comb width and matings	— 0.1846
Comb height and matings	— 0.4303

and the first and third of these being significant.

It is difficult to obtain, from such crude measurements, a function which would truly assess the relationship of comb conformation with mating activity. Comb height appears to be of relatively great importance; it might be expected that comb height relative to the size of the bird would show a closer relationship with mating, but the correlation between mating and the ratio comb height/shank length was only —0.3247. On the other hand a correlation of —0.4972 was obtained between mating and the ratio comb height/comb width, confirming the impression that high and floppy combs are most frequently associated with a lower sex drive. Furthermore, there is a correlation of —0.5055 between mating and comb index (=height/width) calculated from the 15 dam-family averages of these variables and one of —0.6368 from the six sire-family averages. It is thus necessary to test if the significance of differences in mating frequency is merely a reflection of comb size, but statistical analysis (B.M. 3) showed that even after correction for linear or quadratic regression on comb index

the variation between cockerels remained highly significant. In other words the variation between cockerels in mating activity cannot be wholly explained on the basis of a simple relationship with comb size. As evident from B.M. 3 and a graphical picture of the results, little would be gained by fitting higher degree curves.

Finally, it appears that in spite of the high phenotypic correlations quoted above there is little evidence of any *genetic* association between the two characteristics. For the 27 cockerels involved the mating variations follow the familiar pattern found in the whole data. Variation between cockerels is significant and the apparent genetic variance is reflected in significance between sire families. On the other hand for comb index neither male nor female parent produces any significant effect, any slight tendency towards a real effect corresponding to the influence of the female parent (B.M. 4). There is thus the strong suggestion, bearing in mind the limitations of the data, that the phenotypic correlations are environmental rather than genetic in origin, and, apparently, are insufficient to account at all for the genetic variations in mating frequency or to account completely, as the regression analysis shows, for the individual variations which are partly genetic and partly environmental in origin.

Discussion

The significant differences in the sexual behaviour of the different sire-families strongly suggest that such differences have a genetic basis. Although the fertility tests were not rigorous, the evidence from them suggests that the sexual behaviour and fertility of the tested cockerels were correlated to a fairly high degree. It would, therefore, be of considerable interest—both in the academic and applied senses—to pursue the study further, and to obtain from more extensive data estimates of heritability of the two characteristics and genetic correlation between them. Their semen production, however, showed a very inconsistent pattern which might have been due to the following causes vitiating any relationship with sexual activity. Parker, McKenzie & Kempster (1942) found that when semen was collected at intervals varying from 8 days to 6 hours, the sample, judged by its volume and sperm density, declined in quality as the interval between collections decreased. The cockerels used in this study had all been exposed to females at various times before the collections, and thus the interval between their last natural ejaculation and the date of the collection may have influenced the quality of the specimens. Secondly none of them had previously been used for semen collection and were therefore unused to such handling. Under such conditions, docility would be the most important factor and the semen samples of the cockerels probably reflect this to some extent.

As stated earlier, the cockerels used in the fertility tests were all producing semen at that time, and it is unlikely that the differences in fertility were due to differences in semen quality. Apart from possible internal causes of infertility in the hens, their low fertility raises several interesting behavioural possibilities. Firstly, their general receptivity may have been of a low level. Their "bare-backs" due to feather picking has been suggested already as a cause. Another reason may be that these females, who were pullets, had not had a resident male in their pens—consequently the period that the cockerels spent in the pens may have been too short for the pullets to adjust themselves. Wood-Gush (1954) showed that hens and pullets exercise a certain amount of preference which is based not only on the behaviour of the male, but also on other factors, including possibly, physical ones such as size. Furthermore, it will be seen from the statistical analysis that (B.M. 2) female initiated mountings were comparable to other types in their contribution to significance. Actually, in Pen A the significance due to this type was second only to that due to treadings. Therefore, it is fairly likely that female preference, based on behavioural and physical attributes of the male, was another factor operating. These factors, if operating would additively tend to lower the fertility of the less popular and less active cockerels.

It would have been profitable also to have tested the fertility of the males from the middle of the sexual hierarchy. It is possible that the top ranking males copulated too frequently to allow all their ejaculates to contain good semen, for quite often there was under two minutes between apparently successful treadings in these tests. Hence their fertility may have been lower than that of middle-ranking males.

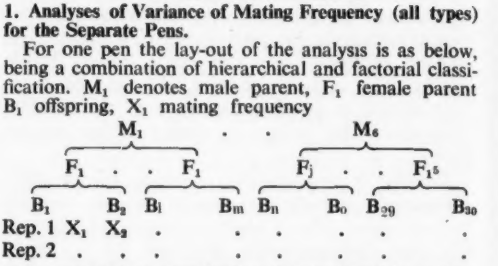
To what physiological and/or psychological processes the genetic differences in libido are due, is unknown. Statistical analysis showed

that whilst comb conformation as defined by height/width, is associated with the frequency of mating, it is insufficient to account completely for the significant variation. To what extent these statistical findings are due to the relatively crude measurements employed is uncertain. Nevertheless, an attempt was made to determine the *modus operandi* of the correlation. Two of the lowest ranking cockerels were observed before and after the removal of their combs. Two of the best cockerels were used as controls. For the best cockerels the mating frequencies as the mean of four replications were 12.50 and 10.25. The two low ranking cockerels tested under the same conditions averaged zero and 2.50. These low ranking males were then dubbed, given several weeks' recuperation in single cages with ample food and allowed to exercise themselves singly in an empty pen to accustom them to any changes in balance due to dubbing. In the repeat test the control males averaged 12.0 and 9.0 respectively whilst the low ranking males, who had gained in weight, showed only slight increases in mating frequency to 1.5 and 4.0 respectively. Such results suggest that the presence of the comb *per se* has only little effect on mating activity. The argument against comb size directly influencing the mating behaviour of the cock by making him generally more sluggish is supported by the fact that no correlation was found to exist between the aggressive tendencies of these cockerels and their mating behaviour (Wood-Gush, Unpublished). It is possible, however, that its effect is indirect by, say, influencing the earlier physiological and/or psychological development of the male. The comb of the castrated Domestic Fowl has long been known to be sensitive to injections of testicular hormone (McGhee, Juhn & Domm, 1928) and likewise the comb of the young male chick (Hamilton, 1938). Therefore, it seems unlikely that the sexually sluggish cockerels, many of whom possessed large combs, were suffering from a lack of testicular hormone. Craig *et al.* (1954) found that some of their rats did not respond to doses of testosterone that were efficacious with others. Similarly Grunt & Young (1952) and Riss & Young (1954) who used male guinea pigs suggested that poor sexual performance was not due to a lack of androgen, but to differences in the substrata or soma on which the hormone acted. It is tentatively suggested that this also is the case in the present material, and it is hoped to investigate this point further.

BIOMETRICAL METHODS

1. Analyses of Variance of Mating Frequency (all types) for the Separate Pens.

For one pen the lay-out of the analysis is as below, being a combination of hierarchical and factorial classification. M_1 denotes male parent, F_1 female parent B_1 offspring, X_1 mating frequency



The replication classification is introduced by a time lag between the first and second set of observations on the cockerels. However, no significant variation is introduced by this factor and there is no evidence of any differential behaviour of the cockerels as regards the two replications. Variations due to replications, interactions of replications with sires and interactions of replications with dams are all insignificant (in fact, on the whole, subnormal) so that the analysis may be abbreviated to the hierarchical classification common in population studies of this type, the two observations per pen being treated as random variables and providing a measure of error variance. Analyses of variance for the two pens are set out in Table III.

Table III. Analyses of Variance of Mating Frequencies

Source of Variation	Degree of Freedom	Mean Square Pen A	Mean Square Pen B
(*a*) Sire families	5	74.50	30.76
(*b*) Dam families within sire families	9	27.83	10.90
(*c*) Full-sibs	15	20.91	11.45
(*d*) Error	30	7.25	3.82
(*e*) Pooled cockerels	29	32.30	14.61

In both cases the "pooled cockerels" mean square is significant beyond the 0.1 per cent. point (*e* tested against *d*) and the full sibs' mean squares are significant at the 1 per cent. point (*c* against *d*). Comparisons of mean squares *b* and *c* indicates the absence of contribution by female parent, whilst in testing for sire influence, 5 per cent. significance is obtained by testing mean square *a* against the pooled estimate from *b* and *c*. Testing of *a* against *b* with only 5 and 9 degrees of freedom, gives 10 per cent. significance in both cases.

2. Discriminatory Analysis

The complications of the analysis in this manifold classification rendered it advisable to carry out a preliminary analysis, ignoring pen and replication effects. A rough idea of the significance of variation between cockerels was obtained from a restricted analysis of variance "between and within cockerels" of the total mountings—$x + y + z + u + v$. The "between cockerels" mean square is 36.83 on 29 d.f. and "error" mean square 7.58 on 90 d.f. with a highly significant F value of 4.86.

Moreover, each of the variables contributes something towards significance. On the above basis the F values obtained for each of the 5 variables, x, y, z, u and v are respectively 1.47, 1.68, 1.39, 1.99 and 2.85. Only the values for y, u and v are significant at the 5 per cent. point (on this very restricted analysis). However, the consistent trend towards significance and the positive correlations found between all five variables in pairs rendered it advisable to include them all. A compromise between this requirement and the computational labour involved in a discriminatory analysis with five variables was reached by using three variables,

$p = x + y + z$, u, and v,

as x, y, and z individually contribute least to significance and moreover, the three-fold classification corresponds well with the previous *a priori* scores

$v = 5$, $u = 3$, $y = z = 2$ and $x = 1$.

The object then was to seek a linear functions $L = b_1 p + b_2 u + b_3 v$ which, taking into account the variances and covariances of all variables, would maximise the "between cockerels" sum of squares as a proportion of the total. Denoting total sums of squares and products calculated in the usual way as p^2, u^2, pu, ... the total sum of squares for the linear compound is

$$T = b_1{}^2 p^2 + b_2{}^2 u^2 + 2b_1 b_2 pu + \ldots$$

and, using the suffix B to denote between class sums, the between class sum is

$$B = b_1{}^2 p_B^2 + b_2{}^2 u_B^2 + 2b_1 b_2 pu_B + \ldots$$

Writing $T/B = K$, the problem is to find values of b_1, b_2, b_3 corresponding to a minimum value of K. Details of the calculations involved are given by Mather (1949, p. 32 *et seq.*) for a similar problem involving ear conformation in barley. The solution for K in this case is 1.63406. In other words $B = T/K$ comprises 61.2 per cent. of the total sum of squares. This represents virtually no increase over the value of 60.9 per cent. obtained from the original unweighted data. Not surprisingly the values of the b's are virtually equal, giving a weighted function of $L = 1.18\,p + 1.08\,u + 1.00\,v$. It is evident that no statistical significance can be attached to the deviations of these coefficients from unity.

3. Correction of Mating Frequencies for Regression on Comb Index

Analysis of variance of the 108 values of mating frequencies for the 27 cockerels gives the following results:

	Degrees of freedom.	Mean square
Between cockerels	26	40.15
Error	81	7.79

The variance between cockerels may be further delineated into a mean square due to linear regression on comb index and one measuring the deviations of regression from linearity. This gives

	Degrees of freedom.	Mean square
Linear regression	1	258
Deviations from regression	25	31.44
Error	81	7.79

Variation due to regression is highly significant ($F = 8.21$). Nevertheless, the deviations mean square is still highly significant ($F = 4.04$) indicating that the variation between cockerels cannot be wholly explained on the basis of a linear relationship with comb index, alternatively that when adjusted to a common comb index the variation between cockerels remains highly significant. Moreover, the significant deviations from linearity cannot be explained on the basis of an underlying simple curvilinear relationship. The increase in sum of squares due to fitting a second degree curve was found to be insignificant, the deviation mean square remaining highly significant at 31.83.

4. Analyses of Variance of Mating Frequency and Comb Index

Analyses of variance for the two characteristics of the 27 cockerels—total mating frequency (sum of four observations) and comb index are given in Table IV.

Table IV. Analyses of Variance of Mating Frequency and Comb Index of Twenty-seven Cockerels

Source of Variation	Degrees of Freedom	Mean Square	
		Mating	Comb Index
Sire families	5	382.00	932.20
"Dams in sires"	9	111.89	1270.44
Full-sibs (Error)	12	104.83	753.00

The mating variations follow the familiar pattern found in the whole data. Variation due to dam is insignificant whilst the sire mean square is significant at the 5 per cent. point when tested against error or against the compound mean square due to full-sibs and dam families. On the other hand for comb index the sires mean square is actually less than that due to dams whilst neither of these mean squares is significantly greater than error.

Summary

1. The mating frequencies of 30 cockerels were studied under uniform conditions. These males belonged to 6 sire families and 15 full-sib pairs. It was found that there were significant differences between the sire families indicating that mating frequency has a genetic basis.

2. When incompleted and completed matings were weighted, these genetic differences remained, and the use of a discriminatory analysis showed that the frequency of all types of mating was a satisfactory criterion of individual behaviour.

3. During the course of mating frequency tests, monthly samples of semen were taken from the males. No correlation was found between the mating rank of a male and the quality of his semen assessed on volume, density and sperm morphology.

4. The five top ranking and five lowest ranking males were tested for fertility and the top ranking males gave the best results as a group.

5. A significant negative correlation (—0.4972) was found to exist between comb index (=height/width) and mating frequency.

Furthermore, there was a correlation of —0.5055 between mating frequency and comb index calculated from the 15 dam-family averages of these variables and one of —0.6368 from the six sire family averages. Further analysis revealed the apparent absence of genetic variability in comb index, suggesting that the correlations were phenotypic only and indicating that the differences in mating activity could not be wholly explained on the basis of comb index. Finally, dubbing failed to improve the mating frequency of two low ranking cockerels to any great extent.

Acknowledgments

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'STRING PULLING' IN BIRDS. 1. INDIVIDUAL DIFFERENCES IN WILD ADULT GREAT TITS

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Introduction

There have been frequent observations of a type of complex behaviour in birds which enables them to obtain food suspended on the end of a thread. The thread may be of such a length that the bird has to hold the pulled-in loops with its feet while reaching with the beak for another pull on the string. These observations, made on a number of species but especially on the Great and Blue Tit (*Parus major* and *P. caerulus*), have been summarised by Thorpe (1943, 1945). More recently Thorpe (1956, pp. 335-9) has discussed observations on a large number of birds showing differences between species and between individuals of the same species. Thorpe suggests, firstly that food rarely occurs in nature suspended on long flexible objects requiring such specialised feeding technique; secondly, that since the food is obtained by manipulation of the string the behaviour may imply "insight" into the food-string relationship (trial and error, or an inborn behaviour pattern may, however, contribute towards it); thirdly that in so far as the string is "used" as an extension of bodily structure it implies a step towards tool-using behaviour.

Altevogt (1953) in some observations on young Blue Tits has described their habit of pulling up and holding long threads, twigs, etc., even though these objects have no food attached. The method of manipulation, pulling with the beak and drawing the object between a foot and the supporting branch is that used by these birds when eating meal-worms. He suggests that string pulling is an innate feeding pattern.

The work described below represents a preliminary study of the effects of external conditions on individual performance in string pulling.

Apparatus and Procedure

The apparatus described by Thorpe (1956) and a similar procedure were used. The birds were kept singly in 6 feet × 6 feet × 6 feet aviaries. On the food table in each was placed the experimental apparatus shown in Fig. 1. This consisted of a horizontal perch approximately 12 inches long to which the string could be attached. The perch rested on a 12 inch glass cylinder of 1.7 inches diameter, in which the string and food were suspended, to prevent the bird from snatching directly at the bait. A piece of red string was looped over the perch, fastened at the side with a drawing pin and hung about 4 inches below the perch. The bait consisted of three sunflower seeds. The birds were kept without food for about one hour before being tested.

Most of the birds were given preliminary training with seeds placed on the experimental perch and subsequently they were tested in half-hour sessions, the sessions usually being separated by 48 hours; the time each bird was observed varied, however, with their performance and is indicated for each one in Table I. Twelve birds were observed in all, out of which only one pulled up the string without further training. An attempt was made to train some of the unsuccessful birds by presenting them with seeds on very short strings and increasing the string length until (at 2 in.—2½ in.) the bird could no longer reach the seed directly.

The birds were all adult, wild caught Great Tits, individually marked by coloured rings; they remained very wild and were easily disturbed. They approached unfamiliar objects placed inside the aviary only after considerable delay. In general, their approaches to the experimental perch were infrequent and short-lived.

Results

In Table I the birds are grouped according to their performance and the results summarised. Individual records of the frequency of approach to the apparatus of nine which responded in the 4-inch string situation are given in Fig. 2, where the responses are also graded according to an assessment of intensity. The main features of both testing and training in string pulling are described in more detail below.

Table I

Bird	Given preliminary training with sunflower seeds on experimental perch	Tested with sunflower seeds on 4″ red string for:	Pulled up 4″ string after:	Took seeds directly from strings measuring:	Pulled up *strings* measuring:	
	Group I: Pulled up 4″ red string without training					
1.	Yes	15 minutes	7 minutes	—	4″ and 5″	Died
	Group II: Trained in string pulling with short strings					
2.	No	i. 70 minutes ii. 35 minutes	—	1″	5″ and 6″	Aviary moved, ceased to respond
3.	Yes	30 minutes	—	1½″, 1″ 1½″	2″, 2½″, 3″, 4″, 5″, 6″	
4.	Yes	30 minutes	—	1½″, ¾″, 1″ 1½″, 2″, 2½″	2½″, 3″, 3½″, 4″, 5″, 6″, 7″	
5.	No	—	—	1″, 2″	2½″, 3″, 4″, 5″, 6″	moved: ceased to respond
	Group III. Training with short strings unsuccessful					
6.	Yes	i. 60 minutes ii. 60 minutes iii. 30 minutes iv. 20 minutes v. 30 minutes	—	1½″		ate only one seed: sometimes tried to fly away with them; sometimes pecked at them only
7.	Yes	i. 20 minutes ii. 30 minutes	—	1″, 1½″	—	no response at all to all to seeds on strings longer than 1½″
	Group IV. No response at all in training series with short strings					
8.	Yes	40 minutes	—	—	—	no response to seeds on 1½″ string
9.	Yes	i. 50 minutes ii. 20 minutes	— —	— —	— —	no response to seeds on 1½″ string
10.*	Yes	i. 30 minutes ii. 30 minutes	—	—	—	did not eat sunflower seeds from ¾″ string. Did not eat loose sunflower seeds placed on perch
	Group V. Abandoned after testing with 4″ string					
11.	Yes	i. 30 minutes ii. 30 minutes	—	—	—	
12.	Yes	i. 30 minutes ii. 30 minutes	—	—		

* This bird was subsequently trained in string pulling by using hemp seeds suspended on black cotton.

PLATE II

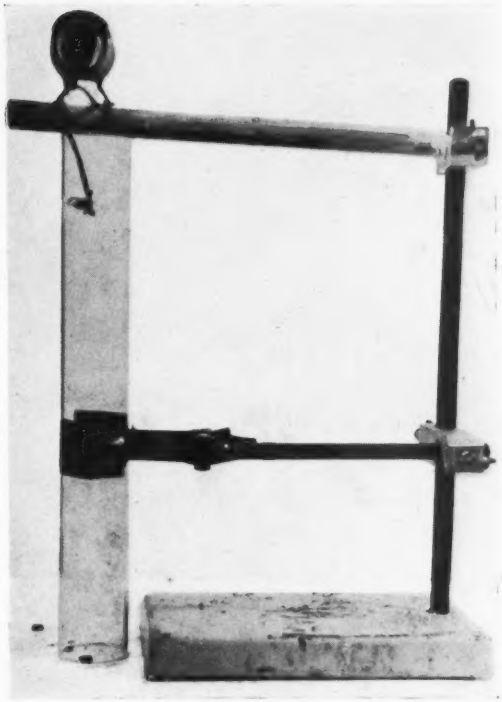

Fig. 1. Apparatus: Bird lifts baited string with beak before putting foot on loop (in this case a hand-reared Great Tit).

* This bird was subsequently trained in string pulling by using hemp seeds suspended on black cotton.

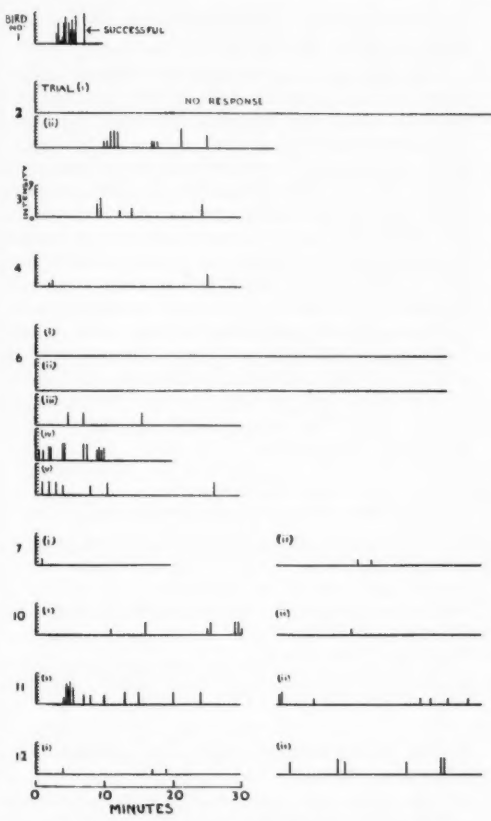

Fig. 2. Individual records showing frequency and intensity of response in trials with 4″ string. Degree of response intensity: 1. alights on clamp. 2. alights on perch. 3. looks towards string or bait from clamp. 4. looks towards string or bait from perch. 5. pecks at glass. 6. flutters round cylinder. 7. pecks at string. 8. pulls at string. 9. pulls string up.

1. The Bird's Response to Bait and/or String Tended to Increase over a Period of Time

The individual records show that in all cases the birds kept away from the apparatus at the beginning of the first trial, and sometimes did not respond at all on the first, or even on the second trial. In general the response to bait and/or string increased in frequency and intensity with the elapse of time. One bird in particular (No. 10) is of interest in this respect as on each successive occasion it alighted on the perch a little nearer to the string.

2. The Bird's Response to the Bait and/or String Subsequently Tended to Decrease

In the 4-inch string pulling situation reinforcement by feeding depended on the bird pulling up the string. Only one bird (No. 1) succeeded in this during the 4-inch trials. The response of the others was unreinforced and it is not surprising that following the initial increase their response tended to decrease in frequency and/or intensity where testing was continued for long enough. This may be seen in the records of Nos. 2, 3, 6, 10 and 11 (Fig. 2). In the cases of Nos. 6 and 11 there is a renewal of more frequent response at the beginning of a new trial.

Nine of the unsuccessful birds were subsequently tested with seeds on a very short string. Six (Groups II and III in Table I) took (but did not always eat) these within 10 minutes; however the three in Group IV (8, 9 and 10) failed to take seeds presented in this way and one of them (No. 10) failed at this stage to take even loose sunflower seeds placed on the perch—this bird was later trained successfully with hemp seeds attached to black cotton.

It may be seen from Fig. 2 that birds varied in the rate at which their response to bait and/or string was built up, in the rate at which it fell off, and also in the extent of recovery between one trial and the next.

3. Some Birds were Trained in String Pulling with Strings of Increasing Length.

An attempt was made to train nine birds, and the course of training is indicated for each in Table I (Groups II, III and IV). The string lengths are there given in order as presented, as when the bird took and ate the bait fairly rapidly the string was subsequently increased in length, while it was shortened when the response was weak.

Under these conditions four birds became proficient in string pulling. An interesting feature of this successful training was that when confronted with a short string (up to 2 in. or 2½ in.) the bird usually took the *seed* directly in its beak, but when lengthened beyond this point the *string* was pulled up and held with the feet while the seed was eaten; and the transition from one method to the other appeared to be effected quite automatically and did not produce any noticeable set-back in the learning other than that usually associated with a small change in the experimental conditions (see below).

Training with seeds on red string was abandoned for the remaining five birds (Groups III and IV), either because they did not respond at all to seeds on short strings, or because this response was weak, and finally ceased altogether.

4. A Change in the Experimental Situation Produced Changes in the Bird's Response

It was observed that the introduction of a change into the experimental situation was sometimes followed by changes in the bird's behaviour. These changes were unfavourable, the response to the string being delayed, or temporarily weakened. The observations were few but may be referred to briefly.

Conditions were changed for three birds which at the time would pull up strings at once, or almost at once. These were carried out as follows:

Bird No. 3.	8.12.52	11.10 a.m. 5 *in. string and* 3 *seeds.* Pulled up at once. Glass cylinder removed.
		11.13 5 *in. string and* 3 *seeds.* One pull on string after one more minute perches and flies away, after three more minutes pulls up string.
		11.23 5 *in. string and* 3 *seeds.* After 10 minutes looks, pulled up string after five more minutes.
	10.12.52	10.15 a.m. 5 *in. string and* 3 *seeds.* Pulled up at once.
No. 5.	14.11.52	10.17 a.m. 4 *in. string and* 3 *seeds.* Pulled up at once.
		10.27.*Two* 4 *in. strings and seeds.* After 3 minutes perched and flew away, after one more, perched, looked at seeds through glass, gave one pull, then pulled up a string.
No. 2.	1.10.52	9.40 a.m. 4 *in. string looped over perch.* Pulled up after 6 minutes.
		10.15 4 *in. string, no loop.* After 7 minutes perched and pecked drawing pin. Alighted on perch after one more minute, again after one more, again after six minutes and nothing more in 15 minutes.

There is additional evidence of the disturbing effect of small changes in the conditions in that increasing the length of the string was also associated with a weakening of the string-pulling response. Five birds were "trained" in string-pulling by the method described above. (p. 111). Altogether there were 26 increases in the length of the string, for all five birds. Results show 10 occasions where the string of increased length was pulled up immediately, or almost immediately (within 3 minutes); 6 occasions where the bird did not respond at all within 5 minutes, and one where a successful response was made but after a delay of four minutes; four where the response was immediate or within three minutes but of very low intensity, e.g. a single pull (one) or simply a look, from the perch (three) and five occasions where a relatively immediate response was made, but a *response of a different kind*, e.g. the bird pecked at the bait through the glass (one case) or alighted on the clamp and/or fluttered round the glass cylinder (four cases). Here it was evident that the response was a direct one, to the bait, rather than to the string.

Lengthening the string acts indeed in the same way as other changes in the experimental situation. The bird does not approach the string in the manner which was previously adequate and is no longer appropriate, but stays away from the experimental perch for an unusually long time or gives a response of low intensity or a different response. It is true that a second presentation of even the same length of string did sometimes produce a weaker response. However, of thirteen such cases examined in the present data, where strings of the same length were presented within a time interval of ten minutes or less, the second response was weaker in only four, and in addition one bird (No. 4) tested on a long series pulled up eight 4-inch strings in 30 minutes.

5. The String Pulling Habit was Lost when the Birds were Moved

Two birds were moved at a time when they readily pulled up 4-inch—6-inch strings. In one case (No. 2) the whole aviary was moved and in the other (No. 5) the bird was moved from one aviary to another.

Subsequently both birds appeared to have lost the string pulling habit although on a single occasion one tweaked at the string. In addition both now failed to eat loose sunflower seeds placed on the perch, although one (No. 5) took to the perch and ate there other seeds found in the aviary. Also hemp seeds placed on the perch were eaten by this bird—while standing as far as possible from the string, close to the retort stand.

It may be that this disappearance of the string pulling habit was temporary only. Experiments with two canaries tested under similar conditions (Vince, unpublished) showed a gradual but complete return of the string pulling response in the course of a few days.

Discussion

The previous history of these adult, wild caught birds was unknown, and the present observations throw no direct light on the individual development of the string pulling habit. However, the responses seemed so delicately dependent upon the external conditions that it is possible that all the birds developed the habit under wild conditions before the experiments began, but that the pattern disappeared under the experimental conditions. On the whole it seems difficult to reconcile either of the hypotheses mentioned above—that the whole sequence is a fairly fixed innate pattern, or is acquired by "insight" into the string-food relationship—with the great variation of proficiency between individuals when first tested, and the extent, again variable, to which their performance improved with training or deteriorated with a change of conditions.

The delicate adjustment on which the pattern seemed to depend is itself of some interest. There was a tendency which varied in different birds for the responses to strengthen initially but then, if the seeds were not actually obtained and the response was not reinforced they died away again. These results resemble those of Grindley (1929). In experiments on the influence of the amount of reward on simple maze-learning in young chickens, he found that chicks given merely the sight of food behind a glass screen ran towards it more and more quickly for several trials, then more and more slowly. This fall in the learning curve he attributed to a process analogous to Pavlov's "extinction" of conditioned reflexes.

The present data support this assumption. The continued presentation of food without reinforcement provides the essential condition for the development of extinction and the following features of the present results are characteristic of this process as described by Pavlov (1927): (i) it tended to develop gradually, (ii) the positive response tended to revive after an interval of time, (iii) in some cases the extinction appeared to extend from the seeds-on-string situation to seeds placed loosely on the perch, or to seeds on very short strings, and (iv) the rate at which the response fell off varied considerably from one individual to another.

The initial rise in the frequency and/or intensity of the Great Tits' response—similar to that found by Grindley in his experiment with chickens—could be due to the dying away or extinction of its fleeing response to a strange object (the seeds-on-string situation, or the food tray in Grindley's experiment). However, it is also possible that merely the sight of food provided reinforcement in the manner of a second order conditioned reflex; in addition the sight of food in association with the perch, glass cylinder, etc., may have contributed to the gradual increase in response strength in view of Grindley's demonstration (*loc. cit.*) that the faster rate of learning associated with a larger "reward" may be increased by association with the sight of the tray from which the food serving as reward was eaten.

Added significance may be attached to the initial strengthening and subsequent weakening of this unreinforced response by the fact that the single successful bird (No. 1) was the one whose responses reached the highest intensity in the shortest time.

The present results indicate that it is realistic to consider the manifestation of an already learned response as dependent on a particular combination of conditions, because here the experimentally established string pulling habit is shown to have been weakened or abolished by changes in the experimental situation. These cases, like the initial delay in responding, appear to be due to the earlier or simultaneous excitation of a different response. The small changes in the experimental situation may well produce a fleeing or avoidance response which is of low intensity and wanes fairly rapidly.

When considered in this way the peculiarities found in the training series become more readily explicable. The very uneven success achieved in attempting to train the different birds may have been due to the fact that the experimental procedure itself deprived the experimenter of control over the reinforcement of the responses. How much reinforcement they received depended in large measure on how strong they happened to be to begin with; once a bird had reached the stage of taking seeds readily from a short string success seemed assured. There was no apparent difficulty for the bird in making the transition from, for example a 2-inch string, where the seed was easily reached, to a 2½-inch string, which must itself be pulled before the seed could be eaten. The birds which succeeded in these training trials could be those whose response to the string and seeds was the most

intense (and it had been reinforced by experience with the short strings); while those which failed could be those still most affected by the extinction produced by the previous unreinforced trials.

Summary

1. Twelve wild adult Great Tits were presented under aviary conditions with seeds suspended on the end of a 4-in. string. The seeds could be obtained only when the bird had pulled up the string.

2. The birds approached the seeds-on-string situation very little at first; then the response was built up slowly and later it tended to die away again if not reinforced by feeding.

3. Only one bird succeeded in pulling up the 4-in. string and obtaining the bait. Four were trained in string pulling by the method of giving food on the end of very short strings which were subsequently lengthened.

4. Changes introduced into the experimental situation were found to inhibit the bird's response to the seeds or string, and could at least temporarily abolish an established string pulling habit.

5. It is suggested that success in this situation may depend in the Great Tit simply on the intensity of the bird's response to the seeds, the intensity varying with external factors.

Acknowledgments

I am indebted to Professor O. L. Zangwill, Psychological Laboratory, Cambridge, and to Dr. W. H. Thorpe, F.R.S., Dr. R. A. Hinde, and Mr. G. E. Dunnett, Ornithological Field Station, Madingley, for their help and encouragement. This work was undertaken with the support of the Medical Research Council.

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A TECHNIQUE FOR THE INVESTIGATION OF CHEMICAL RESPONSES IN AQUATIC ANIMALS

By ALLEN H. BARTEL and DEMOREST DAVENPORT

Department of Biological Sciences, Santa Barbara College, University of California.

Many kinds of apparatus have been designed in the past to test the responses of organisms to chemical stimuli (Thorpe & Jones, 1937; Davenport, 1950; Stehouwen, 1952; Varley & Edwards, 1953; etc.). Of these, several were specifically designed for the study of responses to stimuli which originate at some distance from the organism under investigation. Examples of this type are the Y-tube olfactometer (Thorpe & Jones, 1937; Davenport, 1950) and test aquaria in which animals may be brought under the influence of factors introduced through tubing (Goz, 1941; Walker & Hasler, 1949; Stehouwer, 1952).

It is clear that the design of apparatus used in such an investigation must accord with the behavioral characteristics of the organism being investigated. For example, some animals move too swiftly to test in a Y-tube. Such an animal, when reaching the point of juncture of the arms of the Y, will tend to "overshoot" into one or or the other arm before it has time to make a choice. On the other hand, some animals move too slowly. With such an animal the use of a Y-tube, in which only one individual can be tested at a time, may involve hours of tedious experiments and observations before one can obtain enough data for statistical analysis. In animals such as crabs, which progress sideways, it is impossible to give simultaneous stimulation of symetrically arranged sense-organs with the standard Y-tube. In some organisms it is impossible to elicit any observable, not to say measurable response unless they are in the closest proximity to or even in direct contact with the source of stimuli (Davenport, 1953). Other animals never appear to show as individuals a sharply defined easily observable response which can be objectively recorded. Recently we have developed a new kind of test apparatus which has proven successful in the investigation of the recognition of chemical signals by just such an animal.

We are interested in the behaviour of the hesionid polychaete *Podarke pugettensis* Johnson, which occurs in the free-living state on pilings and under rocks on the southern California coast, as well as in association with the starfish *Patiria miniata* Brandt. There is no discernible morphological difference between the free and commensal individuals of Podarke. In an effort to cast some light on the possible course of evolution of the association habit in this species we have attempted to compare the behaviour of the two populations in relation to the starfish. Even though individuals from neither population show a sharply defined, measurable response to *Patiria*, we nevertheless could demonstrate that a behavioral difference does exist by the simple test of placing a number of individuals from the free population and the commensal population in separate bowls each containing a *Patiria*. Within twelve hours all the commensals were on the starfish, while none of the free-living worms were. In order to demonstrate that the commensal "found" the starfish rather than the reverse we repeated the experiments and obtained similar results when we immobilized the starfish by suspending them within the bowls in bolting-silk bags. These experiments, of course, do not demonstrate any chemical recognition acting at a distance.

Our requirements, therefore, were for a design of "choice-apparatus" which would allow :

1. A large enough number of worms to be testted simultaneously in a single experiment of fixed duration so that a statistically significant result could be obtained even when a number of the worms had not made a "choice".
2. The worms to have adequate time to make free "choice" between sea-water possibly containing host-factor and sea-water containing none, but once having made a "choice", to be effectively trapped.
3. The worms, either by random movement or under the influence of chemical stimuli, to come very close to but never in contact with the starfish until, by being trapped, they had "committed themselves" and could be counted.
4. An easy statistical analysis of the results to be made.
5. The apparatus to be easily adapted for the testing of other sorts of animals or for the experimental analysis of other sorts of behaviour patterns.

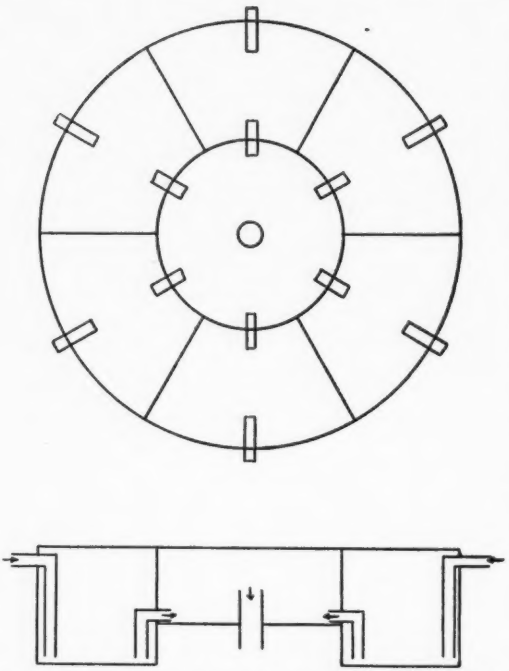

Fig. 1. Test apparatus. Plan (above) and in section (below).

The first apparatus that appeared to us to fulfill the above requirements consisted of a central chamber (a plastic wash-basin) with six radially arranged chambers (plastic finger-bowls). The bowls were connected to the central basin by short Ls of glass tubing (as in Fig. 1) and were kept at a level slightly above that of the central chamber. Water dripped at the same rate into each of these radial chambers caused a slow current to move from each through the glass Ls into the central chamber, which had a central stand-pipe outlet. A worm introduced into the central chamber which entered and passed through one of the glass Ls into a radial chamber would, after coming to the downward directed arm of the L, fall into the radial chamber and be effectively "trapped".

The principle of such apparatus is, of course, the same as loaded dice. If the apparatus is "honest" and no factor which attracts the worms enters from any of the radial chambers, the animals should, provided there are no other effects to alter their behaviour, distribute themselves at random after they have been placed in the central chamber. In four experiments with this apparatus just such results were obtained (Table I). When the apparatus is "loaded" and host-factor enters the system as the result of our placing a *Patiria* in one of the radial chambers, the distribution of the worms should be uneven if they are attracted by this factor. That this was the case with the commensal population is also shown in Table I. Probabilities, calculated by using the null hypothesis that distribution is the result of chance indicated that a significant number of worms were attracted by host-factor.

Repetitive use and washing of the above apparatus (consisting of separate pieces connected by the Ls) resulted in some wear and tear on the holes through which the Ls passed and consequent leakage which affected results. Current investigations are being conducted with a single far more easily manipulable unit (Fig. 1). A "positive" of this unit, consisting of a single

Table I. Experiments with Commensal Population of *Podarke pugettensis* Johnson

Exp. No.	Worms tested	Making no choice	Making choice	Distribution in radial chambers at end of 24 hours							Prob.
				#1	#2	#3	#4	#5	#6		
1.	20	10	10	3	4	1	0	2	0	No star	
2.	19	12	7	0	1	2	1	1	2	No star	
3.	55	18	37	6	7	5	6	7	6	No star	
4.	27	17	10	2	3	0	3	1	1	No Star	
5.	83	15	68	7	10	**24**	11	6	10	Patiria in 3	<0.001
6.	73	20	53	8	8	6	3	**23**	5	Patiria in 5	<0.001

slightly raised chamber with a stand-pipe outlet and six chambers arranged radially around it, was made in plasticene. From this a "negative" was cast in plaster-of-paris. This cast was then repeatedly coated with liquid latex (1P5 Red No. 3 of the General Latex and Chemical Corporation of Cambridge, Mass.). After several coatings the whole was allowed to dry and the latex "positive" simply pulled out of the plaster "negative". This left an unsuspended central chamber and radial chambers separated by thin hollow partitions. Reinforcement of the central chamber and partitions with a wood block and pieces of plywood gave them the necessary stiffness. Occasionally the septa of the radial chambers were found to be perforated with small holes where the "dip" had been too thin. Reinforcement of these with mosquito-bar netting over which liquid latex was painted gave a strong permanent leak-proof wall.

Apparatus of this type has certain great advantages. Once a plaster "negative" is made, one can turn out a number of latex units at will. Such test chambers, with the wood supports removed, can be easily washed and conveniently transported from place to place — indeed, they can be rolled up and kept in the pocket. Modification of the size of the whole unit, the radial passages and the glass Ls will make apparatus suitable to test the responses of many sorts of organisms of all sorts of sizes and symmetries. Such apparatus should prove to be quite as well suited to testing the behaviour of small mollusks, arthropods and chordates as it already has in our investigations to that of annelids.

One word of caution should be mentioned in the use of latex. The liquid product contains ammonia and other substances which may injure or at least affect the behaviour of aquatic animals It was found that leeching the test chamber for two or three weeks in running sea-water removed these factors, tests following this treatment giving excellent results.

The above investigations are being conducted under a contract from the Office of Naval Research. We wish to express our appreciation to Messrs. Egmont Rett and David Hagerbaumer of the Santa Barbara Museum of Natural History for their interest and instruction in the use of latex to make such apparatus.

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PROCEEDINGS OF THE ASSOCIATION FOR THE STUDY OF ANIMAL BEHAVIOUR

An Ordinary Meeting was held on Wednesday, April 25th in the Department of Psychology, Birkbeck College, Malet Street, London, W. C. 1. (by kind permission of Professor C. A. Mace). Professor R. J. Pumphrey, F.R.S., was in the chair and the following papers on the subject of Sense Organs were read.

THE MECHANISM OF CUTANEOUS SENSIBILITY

By P. P. LELE
Department of Human Anatomy, Oxford

It is commonly accepted that free nerve endings in the skin subserve the modality of slowly conducted pain. Studies on the anatomy of cutaneous sensibility, however, have suggested that reports in all four primary modalities, i.e. touch, warmth, cold and pain, are associated with the stimulation of free nerve endings, for complex nerve endings are not present in the hairy skin which covers the greater part of the body.

The human cornea is innervated solely by free nerve terminals subserved by somatic sensory nerve fibres and contains neither blood vessels nor autonomic nerves. The reports which were elicited when it was stimulated under controlled conditions in a number of persons having different social and educational backgrounds were therefore recorded and the results of the experiments were presented.

Since the anatomy of corneal innervation in the cat closely resembles that in man, corneociliary nerve preparations were made in anaesthetized cats and the electrical activity in the ciliary nerves resulting from the application to the cornea of stimuli similar to those used in man was recorded.

The results of these two sets of experiments were discussed in relation to cutaneous sensibility.

THERMORECEPTORS

By R. W. MURRAY
Department of Zoology, Birmingham

There are two methods of investigating sense-organ function: only the behavioural can identify biological value, the electrical method demonstrating mechanisms and coding principles. Logically, behavioural methods should precede electrical methods, but they have not in the case of thermoreceptors. On the basis of an increase in spontaneous discharge with temperature, Hoagland postulated a thermoreceptor function for teleost lateralis organs. In spite of extirpation experiments by Rubin, this has been proved wrong by Dijkgraaf (conditioning experiments). More possible theoretically was the sensitive response to change of temperature in the ampullae of Lorenzini, and Sand postulated a thermoreceptor function for them. But their anatomy, with long jelly-filled tubes from skin to ampulla, makes this improbable, as there is no special thermal conductivity in the jelly. If they are not thermoreceptors, the C.N.S. must be able to distinguish between the proper stimulus and the undoubted result of swimming into water of different temperature. The same problem arises in *Xenopus*. The spontaneous discharge from the lateralis organs shows an adapting response to change of temperature like that of the ampullae, though not so sensitive. Assuming again that the thermal sensitivity is only a byproduct of a mechanism for generating a spontaneous discharge, the C.N.S. must be able to discriminate between activity in single units, caused by entirely distinct stimuli, and this must presumably be on the basis of the temporo-spatial patterns of activity in neighbouring fibres. The single-fibre preparation can no longer be the target for the electrophysiologist's endeavours.

PERMEABLE BASICONIC PEGS IN GRASSHOPPERS AND LOCUSTS

By E. H. SLIFER
Birmingham

No précis of this paper was available at the time of going to press.

LES ORGANES SENSORIELS ANTENNAIRES ET LE COMPORTEMENT DE DIVERS INSECTES

par G. RICHARD
Laboratoire de Biologie Animale S.P.C.N., Faculte des Sciences, Rennes

On a attribué aux antennes des Insectes un rôle important dans le géotropisme et dans la perception de vibrations diverses. Les recherches du Laboratoire dans ce sens ont porté sur le géotropisme de *Catlotermes flavicollis* et sur le réflexe de capture des larves de *Calopteryx splendens*.

On caractérise ainsi le géotropisme des Termites:

1. les imagos sont très fortement géonégatifs au moment de l'essaimage;
2. les larves ne sont pas orientées par la pesanteur;
3. la polarisation géotropique nette s'établit au cours de la vie nymphale du 7 ème stade et les nymphes sont alors très sensibles au degré hygrométrique de leur environnement.

Des ablations d'organes de divers types ont permis de dégager les faits suivants chez les imagos:

1. l'ablation des tarses diminue la précision de l'orientation géotropique et diminue considérablement l'excitation du Termite;
2. l'ablation des antennes diminue de même la précision de l'orientation mais diminue moins l'excitation générale du Termite;
3. l'ablation du segment distal des ailes tend à diminuer la précision de l'orientation et à augmenter l'excitation de l'animal.

Chez les larves, ces ablations ne modifient pas le comportement, sauf en ce qui concerne l'excitation générale qu'elles diminuent.

Des recherches d'anatomie sur l'organe de Johnston nous ont montré qu'il ne subit pas de variations très importantes au cours de l'ontogénèse.

Nous avons combiné de diverses manières le géotropisme et le phototropisme, ce qui permet de préciser les conditions dans lesquelles a'actualisent les diverses phases du comportement d'essaimage des Termites.

Au cours de ses recherches sur le réflexe de capture des larves de *Calopteryx*, Jean Vasserot a pu montrer que le comportement de chasse de ces Ondonates était fondamentalement différent de celui des AEschnes. Chez ces dernières le réflexe d'extension du masque est déclenché par des excitations visuelles; chez *Calopteryx*, au contraire, ce sont des stimuli vibratoires perçus par les antennes qui induisent la capture. On a pur montrer qu'il s'établit, dans certains cas, des suppléances physiologiques entre antennes et tarses et montrer comment des excitations antennaires de même ordre (vibrations) peuvent s'extérioriser par des comportements différents.

HEARING AND VIBRATION SENSE IN INSECTS

By P. T. HASKELL
Anti-Locust Research Centre, London

Hearing and vibration senses in insects are frequently mediated by the same receptors. The sense in general seems to be connected with behaviour patterns leading to contact between the sexes and so ultimately to mating. Nervous discharges in afferent fibres must thus afford some basis for specific recognition and discrimination: in Diptera, the flight note response is mediated by Johnston's organ, but no data on the type of discharge is available. In Orthoptera and Cicadidae, the nervous discharge in the tympanal nerve is related to the pulse repetition frequency of the sounds emitted by the insects. The Orthoptera have in addition to tympanal organs, at least two sorts of hair receptor, one capable of responding synchronously to pure tones, the other of signalling duration of supra-liminal stimuli. Work on

Orthoptera and Cicadidae has shown that specific stridulation differs in the character of pulse repetition frequency and thus it is reasonable to suppose that this is the characteristic on which discrimination is based. Discharges in the tympanic nerves of Lepidoptera differ from those of Orthoptera and Cicadidae by showing adaptation to a constant stimulus; the organs are fitted to receive short bursts of very high pitched sounds, responses up to 70 kcs. having been recorded. This would enable the organs to mediate an echo-location response, but no evidence is available concerning sound output of Lepidoptera; a further theory concerns the avoidance of predators such as owls and bats, which emit short pulses of high frequency sounds while hunting.

Most insects have sub-genual organs in the legs, capable of detecting vibrations of the substrate of molecular amplitude; no information on the nervous discharge of these organs is available, and it is difficult to imagine their purpose, since owing to their extreme sensitivity they will probably be in a state of continual stimulation even in the quietest environment.

VISUAL PERFORMANCE AND THE SIZE OF THE VERTEBRATE EYE

By H. BARLOW
Physiological Laboratory, Cambridge

The physical properties of light impose definite limits on visual performance, and the position of these limits is affected by the size of the eye, and also by its shape. A pupil of large diameter traps more quanta of light, and hence, other things being equal, allows dimmer objects to be seen. A large pupil can be achieved by increasing the size of the whole eye, or by increasing relative aperture; the latter will be more effective if thresholds are limited by retinal noise because the light will be concentrated in a smaller area. A large pupil also allows better resolution, because of the limit set by diffraction at the pupil, but the limit set by chromatic aberration gets worse if the relative aperture is increased. Hence pupil diameter increase allows better resolution, but focal length must be increased more than proportionally to prevent chromatic aberration nullifying the gain.

The physical properties of light thus present obstacles to the evolution of greater sensitivity and acuity. The obstacles must be seen in order to make sense of the different paths that have been followed round them.

BOOK REVIEWS

Birds Fighting. By S. SMITH & E. HOSKING. London: Faber & Faber. 1955. Pp. 128, 62 plates. 18s.

Sub-titled "Experimental Studies of the Aggressive Displays of some Birds," which is a better indication of its contents, this book, which is informative and readable, is divided into two parts. The first, entitled "Adventure with a Stuffed Cuckoo", consists of five chapters describing original experiments designed to determine the reactions of some of the smaller birds (willow warblers, nightingales, robin, chats, pipits, wood warblers, chiffchaffs, sedge- and reed warblers, wood warblers, blackcaps and garden warblers) to a dummy set up in their vicinity. The final chapter of this part sums up the experimental evidence obtained. Part two considers, in seven chapters, Intra-specific Aggression in a variety of birds (ringed plover, oystercatcher, sandpiper, snipe, stone-curlew, greenshank and redshank, wheatear and avoccat). We learn, in Chapter 12, that no reaction was observed in a blackbird when a stuffed cuckoo was placed near its nest which contained half-grown young, but on the substitution of a dummy jay the male blackbird "dashed down on the dummy's back, clawing and pecking at its head," it "then stood on the back of the prostrate dummy for eight minutes doing little else but just stand there, before going off for more food." Nightingales were more afraid of a dummy jay than of a sparrow-hawk as they attacked the latter but withdrew from the former. The same thing happened with whinchats and three pipits which attacked a dummy cuckoo but avoided a dummy jay. In a general review of the experimental results, and the interpretation of them, the author summarises the following points: that the stage reached in the breeding cycle of birds has a profound effect on the manner in which the birds react towards a cuckoo, and the intensity of this reaction, but considerable variations occur between indivudual birds of the same species in the activity of their attacking reaction. The head of an intruder bird is the part that evokes reaction. Recognition of different kinds of predators is clearly shown and reaction to these different predators show well-defined specific differences; this specificity of reaction to a cuckoo is revealed most clearly by the unusual cries of attacking birds. Birds apparently retain a "high retention of visual images, which become deeply 'imprinted' on the bird's consciousness. If the appropriate attacking drive is released by some cause, they will attack the spot where the enemy has been some days previously." In consequence, there is a ready conditioning of birds to a given situation which complicates experimentation. Solidity and correct patterning are essential features in evoking reaction but whether colour, too, plays any part has yet to be proved. Again, "identical displays can belong correctly and unambiguously both to the situation of defence and of nuptials" and, therefore, we cannot conclude that a bird is misinterpreting a situation. Distraction displays occur in abnormal situations that 'confuse' the bird and "fear may then so closely balance the desire to attack that the drive within the bird 'sparks-over' into an incongruous activity". Such are the empirical findings: the authors then consider how these results may be interpreted with a view to shedding light on the mind and psychology of a bird. They modify a statement of Descartes in applying it to birds and say 'I *see*, therefore, I am', since birds are dominated by visual stimuli. They argue that "the dominance of a particular sense may change the interpretation of the external world by a particular animal and make it difficult for us to gain an insight into that world." We must be cautious in our reasoning when we look for analogies with our own interpretation of this world. The revolt against anthropomorphism has "removed from our hands a useful, if dangerous, tool for aiding the interpretation of animal behaviour. Aggression in birds stems from a number of situations that are, in the main, surprisingly similar to those that cause aggression in man." Much has yet to be done since the experimental approach to the study of ethology is in its infancy and "adequate comprehensive theories", founded on basic facts and experimental data, are not yet available. A useful bibliography and index follow an appendix which deals with the statistics of the number of trials necessary to give a significant result. The book contains many beautiful photographs.

C.H.-S.

Zeitschrift für Tierpsychologie

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4

FEAR RESPONSES IN *Emberiza* Spp.

By R. J. ANDREW

Madingley Ornithological Field Station, Department of Zoology, University of Cambridge

The tendency to give fleeing and related responses is one of the main tendencies controlling the behaviour of animals. Here it has been termed, for brevity, "fear." In this paper various types of behaviour given in fear by *Emberiza* spp. are described, and explained as expressing one or more of five subsidiary tendencies:* to flee, to hide, to freeze, to watch the feared object, and to give certain calls (Andrew, in press a). In addition, resting attitudes and movements of the contour feathers which are given irrelevantly during fear, are discussed.

The following account refers indifferently to the Yellowhammer (*Emberiza citrinella*) and Reed (*E. schoeniclus*), Corn (*E. calandra*), Redheaded (*E. bruniceps*), Gosling's (*E. tahapis goslingi*) and Lapland Buntings (*Calcarius lapponicus*), except where otherwise noted. The birds were observed in the field or in aviaries (Andrew, in press b).

1. Alarm, Avoidance and Curiosity

(a) Alarm. This term is taken from Nice & Pelkwyk (1941) who use it to describe similar behaviour in *Melospiza melodia*. In alarm, the bird's neck is elongated so that the head is raised upwards. Sometimes the body becomes upright and the legs are extended in the "tiptoe" attitude (Fig. 1.1). The object may be fixated with both eyes, or the head may turn slightly from side to side. There are frequent tail-flicks and sometimes incomplete take-offs; the species which possess the "tit" flight call (Andrew, in press, a) give it frequently. The crest is usually slightly raised. Caged birds may be alarmed by almost any strange stimulus; if it is sudden, a "startle reaction" (i.e. a single incomplete take-off) may be given first. Fleeing (or freezing) may follow, before alarm begins. In the field, alarm responses may be given as a male hesitantly approaches a female, or in response to man or other predators. Females carrying nest material often show alarm to stimuli which would normally be ignored. Thus a caged female Reed Bunting observed from a hide showed alarm when she was approaching the nest with material but not when she was leaving it.

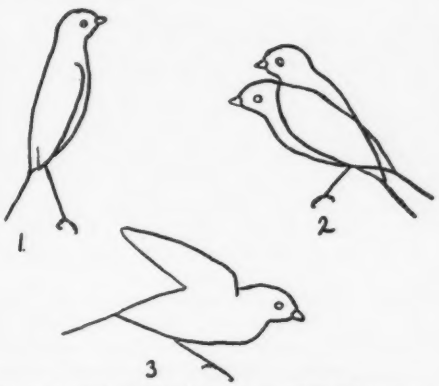

Fig. 1. 1. Tiptoe attitude in alarm (Yellowhammer)
2. Lowering head in mobbing (Yellowhammer)
3. Distraction display (Reed Bunting)

Alarm occurs when there is a weak tendency to flee, opposed by some other tendency (probably to watch the feared object). It is therefore not surprising that many components of alarm should express a tendency to fly (e.g. tail flicks and flight calls). The "tiptoe" attitude is very like the phase of an incomplete take-off in which the body is thrust upwards (Andrew, in press, c). Like this movement, the "tiptoe" attitude is usually held only briefly. An alternative origin for the "tiptoe attitude" is from the posture a bird assumes when trying to see over obstacles. Many animals when startled raise the head as high as possible to look about, (e.g. rabbit). In either case, neck elongation is now partially emancipated from its origin, since it is retained when the legs are somewhat flexed as well as when they are extended. In most situations it indicates fear.

(b) Avoidance. As fear decreases alarm responses cease. The bird may then resume its normal activities; but if the frightening object is still in the cage, its neighbourhood will be avoided.

(c) Curiosity. An alternative response as alarm ceases is for the bird to approach the feared object hesitantly and peer at it with

*When a response occurs it is said here to "express" the tendency to give the group of responses of which it is a member, even if its performance does not appear to decrease the tendency (e.g. aggressive or fear responses)

neck elongated. Later the bird may peck it without giving any fear responses. Here the bird is showing a tendency to explore (curiosity).

2. Mobbing

"Mobbing" is used here of behaviour in which all the components of alarm are given but with the addition of lateral body swings. These, which are never very marked or regular in Bunting mobbing (Hinde, 1954a, and personal observation), are often accompanied by obvious head lowering and raising (Fig. 1.2). Some times calls which express fear are given. Mobbing appears to be a higher intensity form of alarm. In the field, Corn and Reed Buntings were seen mobbing perched Kestrels; and Yellowhammers, a man near the nest. The mobbing birds would approach to within 3 or 4 feet of a Kestrel and sometimes even fly over it.

Hinde (1954 a) has shown that the body swinging of mobbing in *Fringilla coelebs* is derived from movements of turning to flee, in a conflict between tendencies to approach and to retreat. It is likely that it has the same origin in the Buntings, which mob during a similar conflict (cf. Andrew, in press, b). The head lowering may derive from the similar movement of a take-off crouch.

Both body swinging and head lowering may help to obtain by parallax information about the distance of the object mobbed. In Buntings, the side to side turns of the head in looking at the object can be distinguished from half turning away from it, and then turning back. Possibly the former movement originated independently as a movement for obtaining parallax, and now has its function sometimes taken over by body swinging (see also Marler, in press).

3. Freezing and Hiding

(a) Freezing. In freezing, a bird is quite motionless except that it turns its eyes and after a little its head, as it looks around and upwards. A bird may freeze in a normal perching attitude or, if the freezing was preceded by a startle reaction, remain in the initial crouch of an incomplete take-off.

Freezing is aroused in particular by unlocated causes of fear (which explains the bird searching its surroundings with its eyes). Thus it often follows a startle reaction to a sudden noise or is given in response to the "see" fear calls of other birds. Exceptionally prolonged freezing reactions were given by caged birds in response to an unusual silence. Birds hiding in cover often also freeze.

(b) Hiding. Caged Corn Buntings and Redheaded Buntings usually rushed and hid in thick cover at an outside disturbance. All the Buntings would eventually cease fleeing and hide if closely pursued.

4. Responses to Enemies Near the Nest

These responses are considered here since, in the Buntings, they chiefly expressed fear.

A. General Responses

These were of three main types: alarm responses, certain calls expressing fear, (Andrew, in press, a) and remaining motionless in a normal perching attitude watching the intruder. This last response was probably associated with weaker fear than alarm, since it was usually replaced by alarm if the intruder approached closer. In general the responses seemed to be given when the bird had incompatible tendencies to go to the nest to brood or feed the young, and to flee. Yellowhammers, Corn and Reed Buntings gave calls expressing fear during alarm responses, and were usually silent when motionless. Ortolans usually continued to call when motionless.

These four species may be ranked on the distance to which a man must retreat, before they will go to the nest to feed young. The Reed Bunting goes at the shortest distance, then the Yellowhammer and Ortolan, and then the Corn Bunting.

B. Distraction Displays

(a) Reed Bunting. The display, which is silent, usually commences by a very short flight down from the nest with the tail spread wide. A series of short flights alternating with movement over the ground, carry the bird away from the observer. The tail is spread throughout. During the flights, the wing beats are of small amplitude and short glides often occur so that the bird moves only slowly forward. In the movements over the ground the wings may be fluttered, held by the side, or raised to almost full elevation and extension (Fig. 1.3). The bill is sometimes slightly lowered. Howard (1929) described the rump feathers as markedly raised; in the present study the body feathers were either normal, or all were slightly raised.

The display is prolonged if the bird is followed. At some distance from the nest it ceases and the bird perches, silent and usually hidden.

The display may begin again if the observer approaches. Once, in such a pause, the bird's head dropped as if it were about to faint (cf. birds fainting in fear, Armstrong, 1947). Usually, a little after the end of the display the bird returns to the nest; if the observer is still visible it gives alarm responses.

Females put off nest containing eggs or young which they had been brooding usually displayed; occasionally they simply flew away. Twice, males which had been feeding young, or brooding, displayed. The display thus occurs when birds simultaneously have strong tendencies to flee an enemy near the nest, and to return to the nest to brood (or to feed young). Simmons (1952), however, suggested that most distraction displays are caused by a conflict between tendencies to flee and to attack. Perhaps this occasionally applies to the Reed Bunting. Although no aggressive responses to intruders at the nest were observed in the present study, Simmons records that a brooding female once seized the nose of a rat. (Marler, (in press) notes that the evidence that predators commonly arouse aggression in small passerines is scanty). In either case, the essential feature is probably that the tendency to fly away from the observer is opposed by some other tendency.

Nearly all the components of the display are movements of impeded flight. Both small amplitude wing beats and glides result in slow movements, whilst moving over the ground with wings fluttering or raised indicates a strong but thwarted tendency to fly. The tail is always spread during slow flight to prevent the hind end of the body from sinking at this slow air speed. In the Yellowhammer tail-spreading between flights appears to indicate a tendency to fly slowly (Andrew, in press b). The slight feather raising may be caused by fear (below).

A display which resembled the distraction display in consisting of impeded flight, was once seen when the nestlings first left a nest. The female repeatedly flew a short way with spread tail and slow wing beats, followed by a nestling for part of the way; each time, she returned, landed in front of it and flew forward again as before.

(b) Other Buntings. In about a seventh of the occasions on which female Yellowhammers were put off the nest, they flew rather slowly with a spread tail. Usually they landed nearby with their tail still slightly spread and then flew away. In the other cases, they flew swiftly away to some distance, as soon as they were put off. Crouch (1948) notes a distraction display in which one wing was trailing.

The Ortolan often shows hesitant flight, or running, when put off the nest (Géroudet, 1951). A display in which the wings were drooped has been observed in the Cirl Bunting (Zumstein, 1927).

The Corn Bunting was only observed to fly normally away from the nest. Walpole-Bond (1952) states that the female may flutter along the ground but rarely spreads the tail. The Rock Bunting, a relative of the Reed Bunting, gives marked distraction displays which consist of running with extended, usually beating wings (Géroudet, 1954). Carpelan (1932) reports a distraction display for *E. rustica* and Sulpin (1931), for *E. rutila.*

(c) Parulidae. Spread tails and wing flutterings occur in the distraction displays of *Dendroica coronata* (Bent, 1953, p. 24), *D. fusca* (Bent, 1953, p. 343), *D. pennsylvania* (Skutch, 1954), *D. virens* (Pitelka, 1940), *Helmitheros vermivoros* (Bent, 1953, p. 38), *Seiurus noveboracensis* (Bent, 1953, p. 481) and *Setophaga ruticilla* (Skutch, 1954). *Oporornis agilis* may fully extend its wings vertically upwards (Bent, 1953, p. 515).

(d) General. Both the Parulidae and Emberizinae show a distraction display originating from impeded flight. It is interesting that the two groups are probably closely related (Tordoff, 1954). Armstrong (1954) points out that injury feigning tends to occur in birds whose habitat offers open spaces on which to display, and whose nests are accessible to non-avian predators. The Reed and Rock Buntings possess both requirements and display vigorously; the Corn Bunting lacks the first (Andrew, in press, b) and does not. The Yellowhammer, however, fulfills both requirements, sometimes shows impeded flight, and yet very rarely gives a display.

5. Interspecific Differences in Readiness to Give Fear Responses

The Reed Bunting, Yellowhammer and Corn Bunting show, in that order, a decreasing readiness to approach the nest when an observer stands nearby (above). Show judges lay greater emphasis on "steadiness" in exhibited Corn Buntings than in other Buntings because it is more difficult to produce.

In a series of experiments on each of these species, four hand-reared birds of a single species which were kept together, were deprived of water for 150 minutes. A water dish was then put in with a lump of plasticine on its rim and the time at which each individual drank for the first time was noted; if one had not drunk at the end of the observation period then its time was taken as the length of the period. All the birds showed fear responses to the plasticine at first. The Corn Buntings habituated more slowly than the Yellowhammers, and the Yellowhammers more slowly than the Reed Buntings. Their mean times before drinking were significantly different ($p. .05—.02$ for the first and second species, $p. < .001$ for the second and third).

The experiments were necessarily rough since the effect of 150 minutes deprivation of water is likely to be greatest in the smallest bird, the Reed Bunting. They tend, nevertheless, to confirm that the species differ in the ease with which fear responses are aroused, and in their persistence.

6. General Discussion

"Fear" has been used throughout the present study to indicate a tendency to give a group of responses, the chief of which are hiding, freezing, fleeing, fear calls and watching the feared object. In the Buntings it may be compared to aggression (Andrew, in press, d) in that it is aroused and maintained by certain external situations, and that it terminates with their removal. There was no evidence in Buntings that if fear responses were not performed, the tendency to give them increased. "Vacuum" performances of fear responses are, of course, well known in other animals (e.g., ducks: Lebret, q. in Tinbergen, 1951).

Like aggression, fear usually competes successfully for expression with moderate hunger. After 75 minutes starvation, Buntings fly up from the food dish at a disturbance and usually leave it immediately when threatened by a superior. Strong fear may prevent the expression of aggression. The primary cause of aggressive responses appears to be a fellow bird coming too close (Marler, 1955, for *Fringilla coelebs*; Andrew, in press, d, for Buntings); yet for the first few minutes after a frightening object is put on the floor of their aviary, Yellowhammers perch and fly very close together amongst the upper perches, but never threaten. Only later do they threaten between alarm responses.

7. Irrelevant Resting Attitudes

A. Description and Introduction

In the full sleeping attitude the head is withdrawn, and turned so that the bill rests in the shoulder feathers. The contour feathers are somewhat raised, the legs flexed and the eyes closed (Fig. 2.1). In resting attitudes the head is withdrawn to rest on the shoulders, but not turned, the contour feathers are slightly raised and the legs are flexed: often the bird stands on one leg and raises the other. The eyes are sometimes half shut or have the nictitating membranes partially drawn across (Fig. 2. 2). Full sleep is often preceded by such resting attitudes, and they often occur when a bird has no other strong motivation (Andrew, 1956 b)

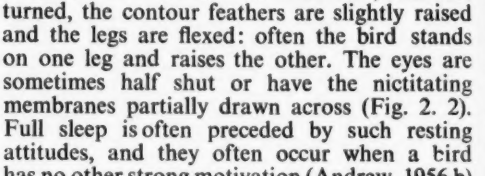

Fig. 2. 1. Sleep (Yellowhammer)
2. Resting attitude (Yellowhammer)

Resting attitudes also occur irrelevantly during fear. They have been chiefly studied in the field, where they were usually recognised by head withdrawal, leg flexion, feather raising and immobility. The eyes were sometimes half closed, or the nictitating membranes drawn. Standing on one leg was never definitely seen but would have been different to detect. These attitudes thus seem identical with normal resting attitudes.

Resting attitudes given by a passerine when afraid of a member of its own species have been shown to serve as submissive postures by Hinde (1952, 1953 a), Morris (1954), and Marler (in press). Here the term resting attitude has been retained since this emphasises their relation to normal resting attitudes, and since, in Buntings, they occur in a number of situations where they can have no submissive function.

B. The Occurrence of Irrelevant Resting Attitudes in Fear

This section is partly based on the analysis of 84 occasions when resting attitudes were given by Yellowhammers in the field. Forty-one of these (20 by females, 21 by males)

were given whilst the mate moved nearby. The bird showed no sign of fear before or after them, and most were probably due to drowsiness. The other cases, and similar behaviour in caged birds or other species, are dealt with below :

(a) After a copulation attempt or courtship. (28 cases). In 18 cases male Yellowhammers flew to a female to attempt copulation, landed, and immediately took up a resting attitude. In 10 cases males which were giving a bill-raised run courtship display (Andrew, in press, b) began to give the display components more and more weakly, to raise the contour feathers somewhat, and to run more slowly, and finally stopped in a resting attitude. In both types of case the resting attitude might be brief or persistent; if it was persistent then the male usually ignored the female's movements and moved no more than a step if she attacked him. Occasionally such resting attitudes persisted for some time after the female left and were resumed on alighting after a brief disturbance. Only 3 of the 28 cases were followed by renewed sexual activity; the rest were followed by maintenance activities, except that sometimes, immediately after the resting attitude, the male hopped away from the female (probably because of fear).

Resting attitudes sometimes followed copulation attempts in Reed and Cirl Buntings but not in the Corn Bunting. Occasionally a female Yellowhammer took up a resting attitude when a male attempted copulation.

(b) During reproductive fighting (15 cases). Male Yellowhammers sometimes took up resting attitudes immediately after an encounter with a rival; so also did male Reed Buntings.

(c) During fear of a bird in the same aviary. Caged Yellowhammers sometimes gave resting attitudes after being attacked by a superior in the winter. In breeding pairs of Reed and Corn Buntings, the male sometimes attacked the female very persistently; as a result she remained for long periods in a resting attitude or assumed a full sleeping posture.

(d) During freezing responses. When a Yellowhammer remains motionless for sometime, intently watching a predator (e.g. man), it often begins to draw the nictitating membrane across the eye. Possibly these movements keep the vision from being blurred by lacrymal fluid and do not indicate a tendency to sleep. However, after a longer time the whole eye is sometimes closed and the bird may take up a resting attitude. Very similar behaviour occurs during Yellowhammer reproductive fighting in birds which, because of fear, are motionless, giving the "see" alarm call.

(e) After fear responses not caused by another bird. In Yellowhammers kept singly or in flocks, resting attitudes sometimes followed immediately after fleeing or alarm caused by an outside disturbance. Corn and Gosling's Buntings sometimes close the eyes, or draw the nictitating membranes across, after fleeing round the cage because of a nearby observer. Often they also assume a resting attitude.

(f) Song. Buntings often sing in a resting attitude; probably this is because they are then inactive. However, contact calls and other responses which indicate fear caused by being alone, often precede song (Andrew, in press, b) and possibly this fear is partly responsible for the resting attitudes.

C. Discussion

(a) Submissive function. Many of the resting attitudes given during fear serve to prevent superiors from attacking. Hinde (1952) and Marler (in press) point out that such an attitude is in many respects the reverse of a head forward threat posture. This may be in part coincidental since all the features in which the attitude is the reverse of that of an active aggressive bird are also those of a normal resting attitude. The bird's reduced activity seems to be of most importance in preventing attack. It no longer attracts the attention of others by moving about, and does not flee (and so give the maximal stimulus for attack) when approached.

(b) Motivation. Hinde (1955) notes that submissive postures occur during thwarted fear in the Carduelinae. Marler (in press) shows that fear is not usually strong during these postures, and that they are associated with "a complete capitulation from fighting." Both only consider resting attitudes given during fear of a member of the same species. In the Yellowhammer, irrelevant resting attitudes are associated with fear, but not always fear of another bird. They are often very persistent, lasting after the object causing fear has gone (above); in such cases they appear to become normal resting attitudes. The unresponsiveness to stimuli which irrelevant resting attitudes share with normal ones, suggests that they as well as the latter may express a tendency to sleep.

If this were so, then irrelevant resting attitudes might be caused by a physiological condition resembling that of a tired bird. Strong fear may be followed by exhaustion quite disproportionate to the preceding exertion: Buntings sometimes collapse after a few minutes pursuit around an aviary, and lie outstretched on their bellies with closed eyes. Resting attitudes may be caused by milder exhaustion. (The lassitude which sometimes follows fear in man may be comparable). Possibly such exhaustion is caused by the after effects of sympathetic activity and adrenalin secretion.

This is clearly not the entire explanation since irrelevant resting attitudes occur most readily during fear due to other Yellowhammers, and may appear very suddenly, and be soon over (e.g. after a copulation attempt). Probably either conditioning or ritualisation has facilitated the production of resting attitudes in these particular circumstances where they serve to prevent attacks.

7. Movement of the Contour Feathers

A. Crest Feathers

(a) Descriptions. Buntings often raise the crown feathers briefly or prolongedly, either alone or together with the nape, throat and cheek feathers. The rest of the body feathers usually remain normal.

In the Yellowhammer and Reed Bunting the number of times the crest was raised in strong, and in weak aggression was compared with similar numbers for fear. Fear was compared with the tendency to behave sexually in the same way. Cases where all three tendencies were probably present were excluded. There were no cases in which fear was definitely not present (itself a significant fact), and so the comparison of aggression with the tendency to behave sexually was not made. The strength of these tendencies were estimated from the behaviour of the behaviour of the birds during, or immediately before or after the crest raising).

Table I shows that crest raising almost certainly expresses a tendency to give fear responses in these two species. Crest raising also appears to express fear in the other Buntings. The Ortolan and Redheaded Bunting frequently raise the crest in fear. The Gosling's, Snow, and Lapland Buntings rarely raise their crests, but each occasionally does so during alarm. The Corn Bunting is similar: only 20 cases of crest raising were noted, and of these 17 were given by caged males after a sexual chase and were accompanied by other fear responses. *Emberiza rutila* (Sulphin, 1931) and *E. rustica* (Carpelan, 1932) raised their crests when a man approached the nest.

Nice (1943) notes that *Melospiza melodia* raises the crest in alarm, and Chapman (1940) that *Zonotrichia leucophrys* and *Z. albicollis* do so when "startled or annoyed." *Passerina cyanea* raises the crest in slight alarm (personal observation).

This motivation of crest raising may be widespread in the passerines. It occurs in *Parus* spp., *Fringilla* and the Carduelinae (Hinde, 1952, 1943a and 1955; Marler, in press).

(b) Inhibition by a tendency to fly. When the body feathers are sleeked because of a tendency to fly, a raised crest is usually sleeked too. This does not occur when the tendency to fly is weak; thus 79/226 crest raisings in the Yellowhammer were accompanied by tail-flicks (tail movements expressing a tendency to fly, Andrew, in press, c). In many cases where a raised crest is sleeked in this way the tendency to fly ex-

Table I. The Motivation of Crest Raising

		Yellowhammer		Reed Bunting	
		Strong	Weak	Strong	Weak
First comparison.	Aggression	45	73	18	44
	Fear	96	34	42	20
Second comparisons.	Tendency to behave sexually	60	125	12	48
	Fear	151	34	40	20

The numbers in the Table refer to the number of occasions when the crest was raised whilst a particular tendency appeared to be strong or weak (see also text).

presses fear; here, two of the responses in which fear may be expressed are incompatible. Andrew (1956) gives other examples of incompatible responses which express the same tendency.

(c) **Function.** The crest is raised so much more often than the body feathers and is so conspicuous when raised that the raising seems likely to be a signal movement; probably it has a submissive function in indicating that aggression is weak.

B. Body Feathers

(a) **Description.** Some feather raisings do not appear to be those of toilet behaviour, of warmth retention, of resting attitudes or of courtship. In the Yellowhammer, out of 32 such feather raisings 18 involved the back feathers, 4 the belly, 2 the breast and 8 all the other feathers. The Reed Bunting, too, usually raises the back feathers in such cases. In both species it is the rump feathers that are most markedly raised in courtship. The Corn Bunting raises its feathers neither in courtship nor in those special cases (cf. the immobility of its crest, above).

(b) **Motivation.** Both the Yellowhammer and Reed Bunting only raise the feathers in this way during agonistic behaviour. In the Yellowhammer about half occurred during intense head forward threat postures, and in general they were given when both fear and aggression were strong. This association with the head forward posture may be partly because a tendency to fly is usually absent during this posture (Andrew, in press, b), and so does not suppress feather raising.

(c) **Relation between crest and body feathers.** The crest is sometimes, but not always, raised when the back feathers are up; if both are raised, then they move simultaneously. The raising of the crest is, however, largely emancipated from the body feather movements; it is perhaps relevant that it can be moved independently in toilet behaviour also (in scratching).

(d) **Discussion.** The raisings of the crest and body feathers dealt with in this section may have been originally part of a general contour feather raising. If so, the back feather raisings mentioned above are probably associated with fear, like crest raisings.

Feather raisings are also of importance in temperature regulation. However, without detailed knowledge of the method of control of feather movements in birds, it is not possible to say whether feather raisings in fear may be directly caused by sympathetic activity, or whether it is necessary to postulate an indirect method of causation, such as Andrew (1956 a) suggested for the cooling responses given during fear, which involve the activity of skeletal musculature.

Moderate feather raising is a warming reaction in the Buntings, and is very obvious when the air temperature falls. On the other hand marked feather raisings in which the feather tips separate might cause cooling by permitting the free circulation of air. This was never observed in Buntings as a response to heated air (Andrew, 1956 a; Wallgren, 1955 a) but Morris (1956) noted it in Estrildines exposed to strong lamps. Possibly the thinner plumage of the tropical Estrildines facilitate cooling by marked feather raising. No attempt was made in the present study to distinguish between these two types of feather raising since the feather elevation varies from moment to moment, and from one part of the body to another. Sometimes the overall effect was one of warning, and perhaps sometimes one of cooling.

Summary

In Buntings, fear responses express five main tendencies: to flee, to hide, to watch the feared object, and to give certain calls.

Alarm, mobbing, freezing and hiding are discussed. Fear responses to predators near the nest, and distraction displays are described.

Resting attitudes occur irrelevantly during fear in the Buntings. They have a submissive function, but are not always caused by fear of another bird. The crest feathers (and more rarely those of the back) are sometimes raised in fear. Possible causes of these types of behaviour are considered.

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THE AGONISTIC* AND COURTSHIP BEHAVIOUR OF THE BROWN LEGHORN COCK

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It has been found (Tinbergen, 1952; Hinde, 1953; Morris, 1954) that display in certain species occurs when the displaying animal is undergoing conflict between different drives. Furthermore, Tinbergen (1952) suggested that display in the fully analysed cases is "a combination of displacement activities and intention movements in simple or more integrated form." The object of the present work is to analyse the agonistic and courtship displays of the Domestic cock, and to compare the two types of display which possess certain common elements (Wood-Gush, 1954). Observations on the cock's display have been done on non-resident cocks that were released into pens of hens for regular periods (Skard, 1937; Guhl, 1951; Wood-Gush, 1954) and it was stated by Wood-Gush (1954) that this display was also performed by resident cocks, but at very much lower frequencies. The factors controlling the occurrence of display by a resident cock therefore offers an interesting problem. In this analysis the term "drive" is used in the sense defined by Thorpe (1951), in which it consists of the complex of internal and external states and stimuli leading to a given behaviour.

AGONISTIC BEHAVIOUR

Materials and Methods

The observations reported here were obtained over a two year period, during which time over 50 different cocks were handled and approximately 300 encounters recorded. The combatant males were mainly introduced into a neutral pen, although occasionally a strange male was put into a pen with a resident cock and his hens. The observer was hidden at all times and the two contestants could see no other birds during the observation periods in the neutral pen. The floor area of each pen was approximately 8 ft. × 8 ft. The analysis of the tendencies associated with the postures, followed, in general, the method described by Hinde (1955). The nature of the encounter, the components of the postures and the direction of any locomotion which accompanied them were recorded. Furthermore, as many consecutive displays as possible were noted so that the actions of the two cocks before and after a given display were known. The number of encounters used for the analysis of each display varied, for the data examined were obtained only from those encounters in which the chances of ambiguity in recording were minimized.

*This term has been defined by Scott & Fredericson (1951) as the general group of behavioural adjustments associated with fighting.

The Agonistic Displays

Introduction

Before proceeding to analyse the individual postures or displays in threat display it is necessary to describe the attacking and fleeing postures.

Strutting. When one cock chases another, he struts (Wood-Gush, 1954). He trails his wings and the tail feathers and ruff may be raised. The legs are slightly bent.

The High-stepping Advance. A cock advancing towards another may carry his head very high, his chest out, his tail high and his wings trailing very slightly. He moves with very high steps. His path is usually oblique and very frequently becomes circular and therefore it is of lower intensity than strutting.

The Fighting Stance. Very often, immediately before fighting, cocks may assume the fighting stance. The head is held low, the legs are bent ready for springing, the neck is often stretched and the ruff raised and the wings are held out in a slightly trailing position, away from the body and ready for springing.

Retreating. When a cock moves away from his opponent but is not in full retreat the head is held up with the neck slightly retracted and the back slopes down to the tail which is depressed. The wings are held in position and do not trail, although occasionally one wing may be raised partially covering the back, and the legs are bent.

The Full Retreat. The neck is stretched forward flush with the back, and the tail may also be depressed, and the wings are flapped as the animal runs away.

None of these postures is entirely absolute. For example, one cock was seen fleeing from its opponent with its head, neck, back and tail flush, and its wings flapping but the ruff raised, an action that is generally confined to aggressive circumstances. Another mixed posture is found when a cock approaches another with his neck retracted or even struts after him with it retracted, for the retracted neck appears in many non-aggressive situations—e.g. when a cock is being feather pecked by his hens, he often stands with his neck retracted. Also it is found when the aggressive drive is waning. Two cocks in the fighting stance may start intention tidbitting (p. 135) and as they do this, their necks may retract.

Fighting may start without any display. Sometimes, one cock runs to a corner and sticks his head into it and lies in a huddled position. The other cock may display immediately, or do so only after he has chased the other and possibly pecked and scratched him a little while he is huddled up. At times, the retreating cock may merely run to and fro next to a wall apparently seeking an escape hole. In these cases, he is seldom closely pursued and the other cock displays before attacking. Occasionally the fleeing cock may eventually also start to display and may initiate the attack. In some encounters, one cock, although never fleeing, may always just keep away from the other cock, and both may display, but their postures may differ and the initiative rests entirely with the one cock. Display is also performed when one or both cocks break off from fighting. If one cock breaks off, both may display, but the other generally maintains the initiative. Display is very prolonged when two frightened cocks are introduced. In a typical example of this, each cock crouched in a corner, giving fear calls, only peering at one another over their backs. After a few minutes, one stood up and then the other rose, and both started to display weakly without moving from their corners. This display was interrupted by periods of mutual observation, and eventually it became accompanied by advances and retreats until after 21 minutes they were fairly close to one another and the one attacked.

This brief description of the types of encounters between cocks demonstrates several points. It is seen that display is absent in pure attacking or fleeing situations. A demoralised cock may eventually recover and attack his opponent, or at leat advance towards him, and in the interim period he displays. Similarly, two frightened cocks after first crouching quietly may then display and finally attack one another. Display is also found when there is no fighting and no capitulation. These points suggest that display occurs when there is a conflict between the attacking and fleeing drives. This contention is borne out by the facts that many of the postures or displays described are accompanied by movements towards or away from the opponent; some advances such as the high-stepping advance are never frontal as in direct attack, but are oblique, or result in a circular path round the opponent. Furthermore, some components of the posture may resemble aggressive behaviour and others, fleeing behaviour.

In the following section, each display or posture is analysed and the data are presented to support the hypothesis that agonistic display by a cock occurs when he is under the influence of these two incompatible drives, attacking and fleeing.

The Displays

(*a*) *The Waltz.* The term was first used by Davis & Domm (1943). The far wing is dropped and the cock advances sideways or circles round his opponent. Variable intensity is found: the wing may be fully or only slightly lowered, and the distance moved may vary. Also the neck may be extended or slightly retracted. It was never performed by a cock that had lost the initiative in an encounter, and it is generally accompanied by some movement towards the opponent; and although the path may be circular, there is no movement away from him. In 91 waltzes analysed, the second cock fled from the waltzer or watched him from a fleeing stance in 63 cases, fought him or assumed the fighting stance in 16, and took no immediate action in 12. In 46 cases, the waltzer followed with an attack on the other bird or chased him, and moved away in only a small number of cases. The waltz, therefore, seems to indicate a fairly high degree of aggression, for it never implies a retreat from the opponent. That the waltzer does not invariably attack indicates that the aggressive drive is still somehow checked and this contention is supported by some records in which a cock waltzed after attacking an opponent who showed no fight, i.e. waltzing appeared with a decline in aggression. Since attack is always frontal it suggests that the waltz, with its "side-on" or circular approach

indicates bridled aggression, although it may grade into a frontal attack. Trailing wings appear in aggressive conditions when the cock is strutting after a fleeing opponent, and in the fighting stance the wings are lowered ready for springing. Thus waltzing contains both aggressive and fleeing elements, although the aggressive ones appear to dominate. Though dealing with motivation, it may be added that the waltz possesses signal function, for in the majority of cases it is sufficient to make the opponent retreat.

(*b*) *Wing-flapping*. Wood-Gush (1954) described this display in its most intense form, but the amount of wing movement is very variable, as is the body stance. A cock may be at his full height or his head may be down flush with his back. It expresses far greater ambivalence of mood than waltzing. An analysis of 97 wing flaps performed in 15 encounters showed that 28 were accompanied by forward steps and 30 by retreating steps; the remaining 39 were performed standing, while moving on a non-committal line, or by first going in one direction and then changing. Furthermore, the orientation of a wing-flapping cock may vary. This ambivalence of mood is further shown by an analysis of the actions preceding and following it in 25 cases from 20 encounters. On 14 occasions, it was followed by an increase in aggressive behaviour and in 11 cases by an increase in escape behaviour or decline in aggressive behaviour. In a number of cases, it was followed by apparently incongruous actions (often incomplete) such as preening, tidbitting, head-shaking, bill-wiping, and fairly frequently by further wing-flapping. It was mentioned earlier that the wings may be flapped as a cock flees, but it is also found during actual fighting; as a cock springs at his opponent to attack him with his spurs, he usually flaps his wings, so that its origin is difficult to determine. In general, it seems to be most evident in those situations where there seems to be a fairly even balance between attacking and fleeing.

(*c*) *Tidbitting*. Davis & Domm (1943) described and named this action. The cock pecks at the ground possibly giving food calls and scratching the ground. It is also very common in the threat display of the cock and is described by Tinbergen (1951) as a displacement reaction. An analysis of 24 observations of tidbitting in 15 different encounters showed that in every case it was followed by a change from advancing or retreating or by a relative increase or decrease of the one drive. This does not necessarily mean that tidbitting changed the motivation of the cock's behaviour, but these overt changes from advancing to fleeing and *vice versa* may indicate a conflict between the drives and thus support the suggestion that tidbitting is a displacement reaction. Like wing-flapping it can be accompanied by advancing or retreating, or non-committal steps, or even a stationary position, with variable orientation. Often a cock may change his direction or movement in single tidbitting action. Very frequently it is incomplete, and this is particularly so when cocks have assumed their fighting stance and their heads appear to be "bobbing." Sometimes, elements from aggressive or fleeing postures may be superimposed. For example, the wings may be held up in the fleeing position.

(*d*) *Feather-ruffling*. Skard (1937) described a posture that "consists chiefly in the cock's raising the feathers of his neck" and called it a weak sexual impulse. Wood-Gush (1954) described a posture called Feather-ruffling in which "the neck is stretched, the ruff is raised, the other feathers are ruffled and the whole body is shaken." These were assumed to be identical, but most probably the posture described by Skard is what Wood-Gush called the Rear Approach.

To the human observer feather-ruffling is very striking, but an analysis of 19 feather-rufflings in 15 encounters shows that the opponent took no overt heed of it. Only in 10 cases was it accompanied by an overt change from advancing to retreating by the performer. In 6 of the cases, it was preceded and followed by tidbitting and preening. In the remaining cases, the performer had merely been watching his opponent, and after feather-ruffling continued to do so. Although the raised ruff and stretched neck may be aggressive elements, in the display, it is most probably a displacement reaction derived from feather settling movements. If however, it is autochthonous then the attacking drive is only very weakly activated. Unlike the other actions so far described, it does not seem to vary much in intensity except that it is accompanied occasionally by wing-flapping. However, further observation may reveal variable intensity.

(*e*) *Head-shaking*. The head is tilted to one side and vigorously shaken with circular movements. This movement can be often over-

looked and possesses the additional difficulty for classification in that it may possibly be a direct response to head irritation. However, in this study, it was never accompanied by head scratching which would be expected in some cases of irritation. It occurred often with allotochthonous movements, principally tidbitting and preening. Occasionally, as in the two previous displays, the bird changed from advancing to retreating. Head shaking of a somewhat different sort occurs sometimes when a cock hears others crowing, but this type is often accompanied by opening and closing of the bill. During the recording of the head shakes for analysis, no crows were heard by the observer and no bill movements accompanied the display. Since any direct autochthonous connections are difficult to detect, it is suggested that it is a displacement reaction. Variations in intensity are apparent not only in the size of the circle described by the head, but also in "vigour."

(*f*) *Tail-wagging*. The tail is moved rapidly from side to side in the horizontal plane. In this data it was the least frequent display. Like head-shaking, it also may serve to counteract some local irritation, but it was not accompanied by preening in the tail region, which one might reasonably expect in some cases, if the irritation was present. Sometimes, it was followed by a change from advancing or retreating, but mostly it was preceded and followed by another display action, the most common being wing-flapping and tidbitting. Its origins are difficult to visualise and it is tentatively suggested that it is a displacement reaction. Differences in intensity are not easily detectable, and it is generally performed when the cock is stationary.

(*g*) *Preening*. Although displacement preening is common in avian species, it was relatively infrequent in this material. Accurate records were available for 15 cases of preening in 11 encounters. Analysis showed that in 5 cases it was immediately followed by increased aggression, but this increase was usually small. In the remaining cases, it was mainly preceded and followed by other displays—wing-flapping and tidbitting being the most common. Sometimes, the bird before and after preening would merely watch his opponent. It was performed while stationary. Differences in intensity were not recorded although the duration of preening would probably be a good measure.

(*h*) *Bill-wiping*. Like the preceding three actions, bill-wiping can be mechanically functional. However, it is performed by cocks with clean bills in situations of apparently conflicting drives. Also, it is often incomplete. Eighteen cases in 14 encounters were fully analysed. In a third of these there was an overt change from advancing or retreating and in the remainder it was preceded and followed by some other posture—tidbitting was most frequently associated, and in approximately half of these cases it followed bill-wiping thus precluding the possibility that the bird wipes its bill merely to clean something off. that had become stuck to it while tidbitting. The allotochthonous nature of bill-wiping, together with the associated actions suggest that it is a displacement reaction. Possible differences in intensity are apparent, even in incomplete movements, for in some cases it is done with much more "flourish" than in others.

(*i*) *Whining calls*. Wood-Gush (1954) called this call the "sex-call," but since it is also heard in non-sexual situations, it is suggested that it be designated the "whining call." It was found to be fairly common in the encounters witnessed and 21 cases from 12 encounters were analysed in detail. Twelve cases were accompanied by a decline or increase in the drive then apparent (either aggression or fleeing). In the remaining cases, there was no apparent change in the animals' aggressive or fleeing tendencies. Occasionally, the call was heard to grade into alarm clucking, but from the data available, it does not seem to be more frequently connected with either an overt decline or increase in aggression.

Conclusions

The above analysis shows that the individual postures or displays are sometimes accompanied by, or immediately preceded or followed by, movements towards, or away from, the opponent. These facts suggest that the bird is in fact in conflict between attacking and fleeing, and the components of some of these postures resemble aggressive behaviour and others fleeing behaviour. Other displays or postures without any obvious autochthonous components are also accompanied by similar movements and appear to be displacement reactions, and so also possibly indicative of an internal conflict between two drives. It seems, therefore, that the agnostic display of the cock occurs when he is in conflict between the two opposing drives, attacking and fleeing. Occasionally, however, display may be due to thwarting of the aggressive drive.

For example, when his opponent is crouching with his head in a corner, the cock may display.

COURTSHIP BEHAVIOUR

Material and Methods

The general observations dealt with here were obtained from watching over 70 cocks for several hundred hours. For the detailed analysis of postures, three cocks and three hens were used. The males were released singly into a pen containing a hen and all the males' movements in relation to the hen were noted. When other experimental results are described later, the procedures used are also given.

The Displays

Firstly, those displays common to both agonistic and courtship behaviour are discussed. Although variable, no absolute differences could be seen between those used in agonistic display and those used in courtship, but a detailed analysis of slow-motion pictures might reveal them.

(*a*) *Waltzing*. As in agonistic display, this posture is variable not only in speed, "fullness" of movements, and components, but in ground covered. It never results in the cock moving away from the hen, although he might do so after waltzing. Of the 137 waltzes analysed, 3 were followed by the cock mounting the hen. This small proportion shows that the sex drive is temporarily weak or inhibited. In 2 of the 137 cases, the male attacked the female with his spurs after waltzing, showing that the aggressive drive is also aroused but is weak or inhibited. In another 3 cases, the male grabbed the hen by the neck after waltzing, and although these actions were probably sexual, aggression cannot be neglected for fighting cocks often peck the back of one another's necks. Despite the low frequency of attacking, waltzing is the only display witnessed that preceded an attack on the hen. Generally it is followed by further display sometimes accompanied by movements away from, or towards, the hen. Whether such movements show changes in the cock's aggressive or fleeing drives, or merely reflect fluctuations in his sex drive due to the hen's behaviour is uncertain. It is suggested that waltzing occurs when the cock is in conflict between the 3 drives.

(*b*) *Wing-flapping*. One hundred and ninety cases were analysed. Two were immediately preceded by mounting or attempted mounting of the hen, indicating an arousal of the sex drive; 52 were accompanied by movements towards the hen and 46 by movements away from her, and the remainder by no movement or by non-committal movements, thus indicating a balance between the conflicting drives. Occasionally, aggressive components such as the raised ruff are found in this display, and similarly submissive postures such as partial retraction of the neck (p. 135) are found. These facts suggest that wing-flapping in courtship occurs when the cock is undergoing conflict between the sex, aggressive and fleeing drives. General observations give the impression that sexually sluggish cocks waltz relatively rarely, but may wing-flap relatively frequently suggesting that the conflict is less intense in the case of wing-flaps compared with waltzes.

(*c*) *Tidbitting*. As in agonistic display, this posture can be accompanied by movements towards or away from the other bird, but in courtship movements away from the hen are more frequent, e.g. 16 cases of tidbitting were associated with movements towards the hen and 48 with movements away from her. In 2 cases it was followed by attempted mounting of the hen indicating a weak arousal of the sex drive. Its allotochthonous character suggests that it is a displacement reaction which is performed when the cock is probably undergoing conflict between the sex, aggressive and fleeing drives, or when his sex drive is thwarted by some external factor(s). In cocks that are moulting or whose sexual activity is low for some other reason, tidbitting is common (Wood-Gush, 1954). In these cases, it is probably an ambivalent movement containing elements of the feeding drive. When intensely performed it is accompanied by calls and hens often run to a tidbitting cock.

(*d*) *Feather-ruffling*. The cock performs this display when stationary and does not always face the female. In a number of cases it accompanied a change from advancing or retiring, but in others it merely punctuated a period of observation by the cock.

(*e*) *Head-shaking*. Like the head-shakes discussed earlier, these postures appeared to be independent of crowing and are unaccompanied by bill movements. Eleven out of the 28 cases recorded were accompanied by an overt change from advancing or retiring indicating the presence of a conflict. The remainder did not appear to accompany any such change, although a conflict was possibly present. For example, one cock is recorded as tidbitting and moving

away, pausing, head shaking and then continuing tidbitting and moving away. It is probably a displacement reaction.

(*f*) *Preening, Tail-wagging and Bill-wiping.* In the 10 single cock—single hen encounters analysed here, no preening or tail-wagging occurred and only 3 bill-wipes were recorded. Two of these were followed by an apparent change from advancing or retiring and the third by tidbitting. As in agonistic display it is probably a displacement reaction.

(*g*) *Whining Calls.* The 3 cocks used in this analysis gave very similar calls, but other cocks have been heard in which the call was rather disjointed and sometimes resembled tidbitting calls, so an objective analysis by sound spectrograph would be desirable. Twenty-eight of the calls recorded were accompanied by direct approaches to the hen, 17 by movements away from the hen and 74 by waltzing. There was also a small number associated with non-committal movements. It seems, therefore, to be most closely linked with conflict situations in which the aggressive and/or sex drives are activated and temporarily outbalancing the fleeing drive.

(*h*) *Circling.* The cock walks round the hen with exaggeratedly high steps watching her all the time, (Wood-Gush, 1954). It is identical in deportment with the high-stepping advance described earlier (p. 133). As in "weak" waltzes the conflicting drives appeared to be in balance although generally this balance did not last long.

(*i*) *Cornering.* This action always leads the cock away from the hen (Wood-Gush, 1954) and his calls almost invariably bring the hen to him—more frequently than in the case of a tidbitting cock—so that it too possesses a specific function, It may possibly be a displacement reaction due to thwarting of the cock's sex drive, but the movement away from the hens and the crouching in a corner resemble fleeing behaviour. Occasionally the ruff is raised suggesting an aggressive component and since it is more common in sexual situations than in agonistic situations, its occurrence may be due to the conflict of 3 drives—fleeing, aggression and sex. However, more details of its components are necessary before it can be interpreted. Once in the corner, the cock stamps his feet and lowers himself to the ground. Wood-Gush (1954) described these movements as resembling those marking the transition between tidbitting and dust bathing. Further observation suggests that these leg movements are possibly more like the leg movements of a cock treading a hen in which case the action may partially be a sexual intention movement. However, a detailed analysis by means of a slow motion film would be necessary to establish this.

(*j*) *The Rear Approach.* This action, which is not present in male encounters, does not always result in copulation even if the hen is receptive and is probably what Skard (1937) called a weak sexual impulse. The cock approaches the hen generally from behind, with his neck stretched and possibly his ruff raised. His deportment is variable; he may hold himself high and move with very high steps, or approach more rapidly with less exaggeratedly high steps and the body kept lower. When cocks are resident in pens containing few hens, this approach is common, but is rarer in the case of visiting cocks. The slow, high stepping posture of the male is very similar to the high stepping advance of agonistic situations when one male circles another, with fleeing and aggressive drives in balance. In the "rear" approach, it appears that the sex drive is the dominant drive, the others possibly being subordinated, although occasionally the ruff is raised indicating some aggression.

General Observations

Occasionally, hens were seen to attack the cock when he waltzed to them, but actual fighting did not occur, for the hens after the initial attack then fled. When small bodied cocks were introduced into pens containing large sized hens, they also attacked the hens, and in these cases the fighting was fairly intense. Male dominance facilitates mating (Guhl, 1950) but generally the cock is extremely tolerant towards hens. It seems however that the more sexually active cocks were much more tolerant to the hens than sexually sluggish cocks. Although the latter cocks seldom fought the hens, they pecked them if the hens tried to pick food off their bills or pick their feathers. These observations support the contention that cocks show a certain amount of aggression towards hens and that this aggression is bridled by the sexual drive of the cock.

The postures of the courting cock include, inter alia, two possibly functional categories; those that may intimidate the hens and those that entice the hens. The intimidating ones include watlzes, which, except when performed weakly, show an ascension of the aggressive and/or sexual drives over the fleeing drive, for the hen generally moves away or crouches to a

waltzing cock. Strutting also belongs to this category. Wing-flaps, although ambivalent, if vigorously performed by an advancing cock, may also belong to this category and also possibly whining calls. The second group includes tidbitting, cornering and also dust bathing. Hens usually join a cock performing one of these actions and possibly they serve to overcome any fear that the hens may have for the cock. The toleration of the cock to the hen's pecks probably serves a similar purpose. The other postures are not easily classified into these categories.

Mechanical Obstruction of Sex Drive

So far, the display has been considered only as a product of conflicting drives, except in certain circumstances where possibly thwarting of the aggressive drive might have been responsible (p. 136). Wood-Gush (1954) suggested that "tidbitting" may sometimes be performed when the sexual drive of the cock is thwarted. It seemed desirable therefore to examine the effect of mechanical obstruction on the cock's sex drive and ascertain whether he displayed in a specific way.

Several cocks were observed singly under obstructing conditions. The roosting board (3 ft. × 5 ft.) of a pen was screened off from the pen by wire netting screen with a large mesh, and thoroughly cleaned so that no grain or droppings remained. Then the cock was placed there in full sight of the hens. The observer was hidden. Most of the actions described previously were performed; waltzing, wing-flapping, tidbitting, cornering, head-shaking, feather-ruffling and bill-wiping, and whining calls. It seems, therefore, that external obstruction of the sex drive e.g. unco-operative hens, can evoke the full display.

Strangeness and Courtship

In small groups living in pens the frequencies of the cock's display is much reduced. Possibly due to the birds' familiarity with one another, the cock's aggressive and fleeing drives are considerably reduced and his sexual drive finds expression without conflict from these drives. Another possibility is that his sex drive finds a ready outlet and thus the conflict is also decreased. It was decided therefore to compare in detail the courtship of cocks in their own and strange pens.

Two cocks were put into 2 pens containing about 10 females each and after 10 days residence the tests began. They were removed from their home pens for 2½ hours and placed singly in a cage, then in the late afternoon they were returned to their home pens and their behaviour during the next 15 minutes was recorded. 2-3 afternoons later, they were again caged singly for 2½ hours and at the same time of day were each released into a strange pen containing approximately the same number of hens as their own pen. Three such pairs of observations on each cock were carried out over three weeks and the results are given in Table I. After this series of experiments the cocks were left in their pens so that the strange birds should not become acquainted. Then after a pause of another 10 days a second series was run. This time the cocks were not separated from their hens at all. When they were tested in a strange pen they were caught, and immediately taken there, and when observed in their home pens they were caught, carried out and reintroduced, so as to minimise the extra variables. The pens used in both series were of identical size and furnishings. The data from the second series is given in Table II. With a 3-way analysis of variance, waltzing was found to differ significantly in the home and strange pens in both tests ($P < .05$), and wing-flapping in test 2. Both were most frequent in the strange pen. The other actions, except whining calls and possibly feather ruffling also tend to follow this pattern, although the data are too few for statistical analysis. It appears, therefore, that strangeness does tend to increase display in general, but when the additional factor of separation, which presumably increases sexual motivation, is added, the difference between the cocks' behaviour in their home pens and the strange pens is lessened. Direct observations suggest that the cock's behaviour is determined by his state of sexual motivation, and by the reaction of the hens to him, rather than by his knowledge of the hens. When a strange cock was introduced to a group of hens accustomed to this experimental procedure, their first reaction was to come forward as he was being introduced as they did with a familiar cock and then, contrary to their general behaviour with a familiar cock, they moved away. If the cock was highly motivated or rough, the hens usually retired to the platform in front of the nests where they were out of reach, and if they gradually returned to the floor they remained evasive. Separation appeared to make the cocks more excited sexually, so that they sometimes became rough even with their own hens who occasionally retired to the next platform, and the cock

Table I. The Performance of Two Cocks in their Own Pens and Strange Pens after 2½ hours Separation from Hens. Bill-wiping and tail-wagging were excluded due to inaccuracy of counts

Cocks	Actions	1st Week		2nd Week		3rd Week	
		Home	Away	Home	Away	Home	Away
P.B.	Waltzes	8	12	1	11	5	18
	Wing-flaps	17	19	2	2	17	12
	Tidbitting	2	5	31	17	2	26
	Cornering	—	3	—	—	—	—
	Whining Calls	9	9	—	2	1	5
	Head-shaking	11	2	6	9	3	3
	Feather-ruffling	1	1	1	1	1	1
H.C.	Waltzes	15	27	6	23	5	15
	Wing-flaps	15	25	8	15	5	15
	Tidbitting	6	1	2	20	5	3
	Whining Calls	47	42	18	26	20	59
	Head-shaking	5	4	—	2	3	17
	Feather-ruffling	—	2	—	1	2	2

Table II. The Performance of Two Cocks in their Own Pens and Strange Pens without Separation from Hens.

Cocks	Actions	1st Week		2nd Week	
		Home	Away	Home	Away
P.B.	Waltzes	—	6	2	4
	Wing-flaps	3	7	1	8
	Tidbitting	—	9	—	1
	Cornering	—	5	—	—
	Whining Calls	1	1	—	6
	Feather-ruffling	2	2	1	2
	Head-shaking	—	—	—	—
H.C.	Waltzes	2	5	4	12
	Wing-flaps	1	14	4	9
	Tidbitting	—	3	—	—
	Cornering	—	—	—	—
	Whining Calls	42	58	31	49
	Feather-ruffling	2	5	2	2
	Head-shaking	1	9	—	7

(In the data on waltzing the interaction between cocks and pens, cocks and weeks, pens and weeks were non-significant and the sums of squares of these interactions were pooled with the error sums of squares to increase the degrees of freedom).

then tidbitted. Generally, however, they remained on the floor and just evaded him if he was rough, but in all cases they regained their confidence as a group much more quickly than the strange hens. These general observations indicate that both separation and strangeness tended to increase the evasiveness of the hens, and it is tentatively suggested that their movements away from the cock either directly aroused his aggressive tendencies, so that he waltzed more, which, it is suggested, is the display possessing the highest aggregation of aggressive components, or that these evasive movements of the hens thwarted his sexual drive and thus caused additional display. Since the cock's behaviour is so dependent on that of the hens, clear cut results for statistical treatment are difficult to obtain. These results, however, do support the suggestion that a resident cock's display is reduced in frequency by the familiarity of the birds and by a ready outlet for the sexual drive. The motivation of his occasional display, however, remains unsolved. It may be that his aggressive drive is occasionally aroused by the behaviour of a hen, or that his sex drive is obstructed by his hen's temporary indifference.

Conclusions and Summary

The display of the threatening cock is very similar to that of the cock introduced to a group of hens. In agonistic circumstances, the basis of the display appears to be a conflict between attack and escape. In the company of hens, the cock's display may also be due to this same conflict, e.g. so many displays are accompanied by movements towards and away from the hens. Close analysis, however, may show that the sexual drive is also aroused, e.g. copulation after waltzing and whining calls. Even if this sex drive is not evident on closer analysis, general considerations make it unlikely that his display is purely agonistic, for normal males very rarely attack females, Furthermore, sexually active cocks not only display more than sexually sluggish cocks, but they are more tolerant towards the hens generally. Since the main differences between such cocks are the strengths of their sex drives, it seems very likely that the sex drive is in part responsible for the increased display and tolerance. Courtship display appears therefore to be due to conflict between sex, attack, and escape, and to differ basically from agonistic display.

The similarity between the cock's display in agonistic and courting circumstances may suggest that instead of having conflict between attacking and fleeing in courtship, there may be sexual elements in agonistic display. This, however, seems to be extremely unlikely due to the fact that no sexual behaviour was witnessed after the agonistic display in the encounters staged during the course of this work. Homosexuality does develop, but only when cocks are confined together without hens. Furthermore, if two cocks are introduced immediately after removal from their hens, they generally display and it is very unlikely that in these conditions they offer one another any sexual stimulus.

During the encounters between cocks it was found that when one cock crouched, the other might display and it was suggested that this display might be due to thwarting of the cock's attacking drive. Furthermore, when a cock was mechanically prevented from approaching his hens it was found that he displayed and that this display was very similar to his normal display. It seems therefore that thwarting of a drive by external factors may sometimes be responsible for part of the display of the domestic cock.

The displays of the cock include at least two categories based on the overt female reaction. The first category appears to intimidate the female, for she usually moves away or crouches to the cock. The second category appears to entice or to pacify the hens. However, not all the males' actions can be easily classified.

The cocks observed in these experiments appeared to display more in the presence of strange hens than in the presence of familiar hens, if they had not been caged for some time. It is suggested that the behaviour of the strange hens either aroused the sexual and aggressive drives of the males simultaneously or that their general evasive behaviour thwarted the cock. Generally, thwarting of the sex drive appears to enhance display and it is suggested that the sporadic display of a resident cock may be due to temporary thwarting of the sex drive.

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DIURNAL MIGRATIONS OF THE ECHINOID *Diadema setosum* (Leske)

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Introduction

Millot (1954) has performed a series of experiments on the responses of *Diadema antillarum* Philippi to directional light and to changes in light intensity, concerning movements both of the whole animal and of isolated organs. In a study of the effect of change in light intensity on the movement of the whole animal, he has demonstrated that the response depends on the light intensity to which the urchin has been subjected for the period immediately preceding the change. Thus a dark-adapted animal avoids light of increased intensity, and a light-adapted one moves away from shade when the intensity of light is reduced. The response is most marked in dark-adapted urchins. Millot suggests that the nervous system, which he has shown to be directly excited by light, is shielded during the day by pigment in superficial melanophores and relatively exposed at night, the animal then responding to very small changes in light intensity

Observations and experiments of the related species *Diadema setosum* (Leske) are described below. This echinoid occurs in numbers at Suakin on the Red Sea coast of the Sudan.

The island of Suakin stands in a lagoon connected to the open sea by a narrow channel almost a mile long. The natural harbour thus formed is no longer used except by a few small native craft during the pilgrim season. The low-lying island is bounded by a cliff which drops half a metre to the water surface and a further one to three metres to the bottom. A search of the sea bed near the island during the day reveals only very occasional specimens, but the tips of the spines of many individuals can be seen in the crevices of the cliff face. At night, the urchins emerge on to the adjacent sea bed, and their dark shapes can be spotlighted with a powerful lamp, when they move out of the beam immediately.

Observations and Experiments

For two twenty-four hour periods during 15th-18th December, 1955, a section of the cliff face, 30 metres long, and its adjacent sea bed to a distance of 3 metres from the shore were kept under observation, and counts were made every two hours of all visible urchins. The tabulated figures (Table I) show that a definite nocturnal migration takes place, the urchins moving out on to the sea bed at dusk, and back into the crevices of the cliff at dawn.

Table I. Numbers of *D. setosum* Observed in Various Situations at Intervals Throughout Two Periods of Twenty-four Hours

	15/16.xii.55				17/18.xii.55			
	Tips of spines visible	Test fully exposed			Tips of spines visible	Test fully exposed		
Local Time	In crevices	On cliff face	On sea bed	Weather	In crevices	On cliff face	On sea bed	Weather
Noon	37	0	0	Gusty, no cloud	36	0	0	Calm, no cloud
14.00 hrs.	32	0	0	"	35	0	0	"
16.00	35	0	0	"	39	0	0	"
17.15	5	38	1	"	10	27	0	"
17.20		DUSK				DUSK		
17.30	17	44	25	Wind dropped. Moon	6	42	21	No moon, calm
18.00	2	41	67		1	40	70	
18.30	3	39	71		4	45	68	
20.00	4	41	83	Moon gone	0	43	82	
22.00	0	41	81		0	41	86	
24.00	0	42	82		0	42	84	
02.00	0	43	83		0	42	78	
04.00	0	42	78		0	44	82	
05.00	0	40	75		0	41	76	
05.30		DAWN				DAWN		
06.00	41	0	0	No sun	38	0	0	Sun
08.00	34	0	0	Sun	36	0	0	
10.00	38	0	0		37	0	0	
Noon	36	0	0		37	0	0	

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Another colony of 27 urchins in the middle of the southern arm of the lagoon was found at night scattered over the sea bed, but retired by day under some submerged metal plates, not a single individual being found on the exposed sea bed. This activity was observed on both dark and moonlight nights.

Fox (1924) showed that the breeding rhythms of *D. setosum* are correlated with the lunar cycle, the gonads maturing between the first quarter and the full moon, when spawning takes place. He gives the breeding season of this species at Suez as ending in September independently of temperature. Since my observations were made 1-4 days after the December new moon, it seems most unlikely that this activity is due to spawning rhythms.

To find to what extent change in light intensity is responsible for this activity, a series of simple experiments was performed on the sea bed.

Six openwork baskets made of palm branches, each containing six urchins, were suitably weighted and sunk to a depth of one metre. The mesh of the baskets was approximately four square inches, so that sea water circulated freely through them. One half of each basket was shaded and the position of the shaded half alternated in the six baskets. Records of the positions of the urchins at two-hour intervals were made over two periods of twenty-four hours. The results (Table II) show that the urchins, which were collected from crevices at 11.30 hours, quickly moved into the shade, remained there until dusk, and then emerged into the exposed half. After 20.00 hours, some of them moved back into the shaded half, the distribution of urchins in the two halves after that time being evidently random until dawn when all moved into the shaded half.

Unequal distribution of food organisms or dissolved oxygen may thus be discounted as causative factors of the nocturnal migrations. The activity of the captive urchins differs from that of the natural population only in the return of some of the animals to the shade after 20.00 hours. This may be the result of random movement in a confined space, which would not occur in the natural population. Diurnal changes in food distribution, dissolved oxygen, current speed and temperature, as well as some inherent rhythm, may equally well account for the results shown in Tables I and II. Further experiments were thus designed to establish the relative importance of change in light intensity and any of these, as causative factors.

Six urchins were kept in each of four fully exposed baskets until midnight when one half of each basket was shaded, the urchins being in the exposed halves. In two baskets the exposed half was illuminated, the intensity of illumination being 40 foot-candles. The urchins in these baskets quickly moved out of the increased illumination into the shaded half (Table III), whereas in the controls only very few did so, and more slowly. In a similar experiment, in which six urchins were kept in each of six completely shaded baskets during

Table II. Number of *D. setosum* in the Exposed Half of Each of Six Half-shaded Baskets, at Intervals Throughout Two Periods of Twenty-four Hours

Local Time	17/18.xii.55						18/19.xii.55.					
Noon	6	6	6	6	6	6	6	6	6	6	6	6
12.15 hrs.	0	0	1	0	0	0	0	0	0	0	0	0
14.00	0	0	0	0	0	0	0	0	0	0	0	0
16.00	0	0	0	0	0	0	0	0	0	0	0	0
17.15	0	0	0	0	0	0	0	0	0	0	0	0
17.20	DUSK						DUSK					
17.30	5	3	3	2	1	2	4	4	3	2	4	1
18.00	6	5	4	6	4	5	6	5	4	5	6	6
20.00	6	6	6	6	4	6	6	6	6	6	6	6
22.00	5	6	4	6	5	5	5	4	4	2	3	4
24.00	4	5	2	3	4	0	2	4	1	3	2	2
02.00	4	1	0	5	2	3	1	2	3	2	5	4
04.00	0	3	4	2	3	5	3	0	3	6	4	4
05.00	3	2	3	4	2	4	4	2	1	5	3	2
05.30	DAWN						DAWN					
06.00	1	0	0	1	0	0	0	0	0	1	0	0
08.00	0	0	0	0	0	0	0	0	0	0	0	0
10.00	0	0	0	0	0	0	0	0	0	0	0	0
Noon	0	0	0	0	0	0	0	0	0	0	0	0

Table III. Number of Dark-adapted Urchins in the Exposed Half of each of Four Half-shaded Baskets, two of which were Illuminated in the Exposed Half after Midnight

	Light		No Light	
24.00 hrs.	6	6	6	6
00.30 „	0	0	5	4
01.00 „	0	0	3	4

the morning, and then three baskets half-shaded and three fully exposed at midday, the urchins in the half-shaded baskets quickly moved into the shade (Table IV).

Table IV. Numbers of dark-adapted Urchins in the Exposed Halves of Three Half-shaded Baskets, and in the Original Halves of Three Fully Exposed Baskets

	Half-shaded			Fully exposed		
12.00 hrs.	6	6	6	6	6	6
12.30 „	0	0	0	5	3	6
13.00 „	0	0	0	3	4	3

The complementary experiment was made in which urchins were kept in direct sunlight for two hours and then six of the nine containers half-shaded. The urchins in three of the half-shaded baskets were originally in the exposed half, those in the other three were originally in the shaded half. Those animals originally in the exposed half tended to stay there, while of those originally shaded, some moved into the exposed half (Table V).

Discussion and Conclusion

The movement away from increased light intensity by dark-adapted animals can be induced experimentally at times other than dawn, and it is probable that in the natural conditions of Suakin lagoon change in light intensity is responsible for the movement of urchins at dawn. There is some experimental evidence of the avoidance of shade by light-adapted individuals, but the response does not seem to be sufficiently well marked wholly to account for the observed nocturnal redistribution of the natural populations. However, this factor may act in combination with others, resulting in the nightly migrations. It is possible that when the light intensity is reduced the effect of other stimuli, notably hunger, is added, causing the urchins to move out into the open. In the natural population the presence of food on the sea bed would tend to keep the animals there until the light factor was reintroduced at dawn.

The more marked sensitivity of dark-adapted animals has been noted by Millot in his studies on the responses of *D. antillarum* to changes in light intensity, both concerning the spine reflex (Millot, 1953, 1954), and movements of the whole animal (Millot, 1954). It is possible that the diurnal screening effect of superficial pigment which he postulates for this species (Millot, 1950, 1952, 1953, 1954), also occurs in *D. setosum*.

In the West Indies, *D. antillarum*, while commonly found in shady situations during the day, may nevertheless occur in appreciable numbers fully exposed to tropical sunlight in a few inches of water. The behaviour of *D. setosum* at Suakin differs from that of *D. antillarum* in showing a more marked avoidance of light during the day. Professor Millot has suggested to me that *D. setosum* may have a more developed photosensory system or be less well protected. It is also possible that the Suakin lagoon, where the calm shallow water covers a relatively smooth sea bed on which no shadows are cast during the day, approaches experimental conditions more closely than the West Indian habitat. The relative lack of temporarily shaded sites on the sea bed at Suakin would make gradual light-adaptation less likely, with the result that fewer urchins would be found in exposed situations during the day.

Observations on both species from other areas would be of great interest.

Table V. Numbers of Light-adapted Urchins in the Exposed Halves of Six Half-shaded Baskets, and in the Original Halves of Three Fully Exposed Baskets

	Half-shaded						Fully exposed		
	Urchins originally exposed			Urchins originally shaded					
12.00 hrs.	6	6	6	6	6	6	6	6	6
12.30 „	5	6	6	3	1	2	6	5	6
13.00 „	4	5	3	2	2	1	6	5	6

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THE EFFECTS OF TESTOSTERONE PROPIONATE ON AGGRESSION IN MALE AND FEMALE C57BL/10 MICE

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Introduction

Sex differences in aggressive behaviour are frequently exhibited among animals. For example, Fredericson (1952) found that out of ten pairs of female mice only one pair fought consistently, and one pair fought once. In a similar situation all ten pairs of males fought consistently.

Sex hormones are usually considered responsible for these sex differences, since androgens can often stimulate aggressive behaviour in both males and females of many vertebrates (Collias, 1944). Gonadectomized male mice cannot be trained to fight; however, when treated with testosterone propionate, they show the normal pattern of aggressive behaviour (Beeman, 1947). With the termination of testosterone treatment, the mice stop fighting. Immature male, but not female, mice will fight when given testosterone (Levy, 1953, 1954). Although the sex hormones are a major factor in the difference between the sexes, Eayrs (1952) has suggested that there may be a "structural difference between male and female nervous systems which renders one more susceptible than the other to the action of specific steroids."

The present experiment was conducted to determine whether there is a difference in the aggressive behaviour of male and female mice, other than the androgen level.

Method

Three groups of mice of the inbred C57BL/10 strain were used: 22 gonadectomized females, 20 gonadectomized males, and 20 intact females. The gonadectomized males and females were operated on at 30 days of age, at which time the intact females experienced a sham operation. At 40 days of age the gonadectomized animals were given a single intramuscular injection of 0.5 mg. of testosterone propionate in 0.25 cc. sesame oil. The intact females were given a single 0.25 cc. injection of physiological saline solution. Mice were paired within each group but housed individually until tested. The age of the mice in each pair did not differ by more than one or two days.

Individual mice in each pair were allowed to come together for five minutes once each day for ten days, beginning on the day they received the injection. The mice were fought in boxes similar to those in which they were raised, except that the partition separating the two 12 in. by 6 in. by 6 in. living cages was removed, thus doubling the size of the fighting cage during each trial. This procedure eliminated the necessity of handling the mice prior to the test. Time to the first fight (fighting response latency), number of attacks by each individual, and number of individuals fighting back were recorded. All fights were stopped immediately to prevent the development of dominance, since the same animals met in each trial.

Results

The testosterone treatment given the gonadectomized females did not cause more aggressiveness than in normal females observed by Fredericson (1952), nor more than the intact females in this experiment (Table I). Fighting occurred in two pairs, both in the gonadectomized female group. The first aggressive responses

Table I. Aggression displayed by Three Groups of C57BL/10 Mice during Ten Trials. The Gonadectomized Mice received 0.5 mg. Testosterone Propionate

Groups	No. of mice in group	No. mice attacking	No. mice fighting back	% of mice exhibiting aggression
Gonadectomized females	22	6	2	36·4
Intact females	20	6	0	30·0
Gonadectomized males	20	10	10	100·0

by gonadectomized females were elicited on the fourth day and the number of individuals participating in attacks or fights increased to five on the final test day.

The testosterone treated males fought significantly faster (Mann-Whitney *U* test yields $P < .001$) than the gonadectomized females treated with testosterone. It was shown by Beeman (1947) that untreated gonadectomized males of this strain will not fight if they have not had fighting experience before gonadectomy. The gonadectomized males fought in 68 per cent. of the 100 trials given to the ten pairs, while the gonadectomized females fought in 6.4 per cent. of their 110 trials. All attacks by the males were followed by a fight.

Discussion

The persistence of the sex differences in aggressiveness under the conditions of this experiment suggest four interpretations.

1. There is a non-gonadal source of androgens, such as the adrenals, which cause the greater aggressiveness in the castrated males.
2. The sexes catabolize the testosterone at differential rates.
3. The central nervous system responds differentially to the hormones in each sex.
4. The stimulus provided by the female's behaviour is less effective in eliciting aggressiveness than that provided by the male.

Testosterone is the most active androgen and is produced by the testes, probably by the ovary, but not by the adrenal (Dorfman, 1955). In young gonadectomized mice of both sexes, it is unlikely that there is a sufficient quantity of non-gonadal testosterone produced to affect the behaviour of the mice. Endogenous production of testosterone from the testes is approximately .06 mg. per day (Chai, 1956). Since the experimental mice received a larger dose (0.5 mg.) of testosterone than they probably received from endogenous sources, it is unlikely that any non-gonadal source is effective in bringing about sex differences in behaviour.

Organic responses to the administration of testosterone propionate in the female are similar to those in the male. The effect of testosterone propionate on the preputial gland, uterus, and adrenals of gonadectomized female rats appears early (third to eighth day) and is progressive when given daily injections of 0.2 mg. of testosterone (Mazer & Mazer, 1940). If the differences in behaviour result from differential rates of destruction of testosterone in the two sexes, it is likely that the effects would be produced in the first few days and then diminish throughout the test period. Instead, the number of gonadectomized females which elicited aggressive responses (attacks) increased after the fourth day.

If testosterone operates by sensitizing preorganized mechanisms within the central nervous system (Beach, 1947), it is possible that males are more sensitized by testosterone than females, or that there is a different organization within the central nervous system of each sex. The results of the present experiment may be explained on the basis of these possibilities.

Social releasers for aggressive responses in mice have not been isolated (Scott & Fredericson, 1951); however, it is known that male C57BL/10 mice rarely attack females and may even inhibit their aggressiveness towards other males when a female is present (Fredericson, 1955). Olfactory cues may stimulate one male to attack another. It is possible that females do not present the necessary stimuli, either behavioural or olfactory, to induce aggressive behaviour. A measure of the aggressive behaviour in male-female pairs would adequately test this hypothesis.

Summary

Young gonadectomized males and females C57BL/10 mice were given one 0.5 mg. injection of testosterone propionate at 40 days of age and tested for their aggressive responses on the succeeding 10 days. The males responded more aggressively towards each other than did the females. The two most likely explanations of these results are that either the nervous systems of both sexes respond differentially to testosterone or that females do not provide as adequate a stimulus for releasing aggressive responses as do the males.

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OBSERVATIONS AND EXPERIMENTS ON EGG-LAYING IN THE BLACK-HEADED GULL *(Larus ridibundus* L.)

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Introduction

An attempt was made to collect some data on egg-laying in the Black-headed gull. Some experiments were carried out as a first step in the analysis of the egg-laying mechanism in this species. As will be seen this work confirms and extends a similar study made by Paludan (1951) on the Herring gull (*Larus argentatus*) and the Lesser Black-backed gull (*Larus fuscus*).

The Ravenglass gullery is on a strip of sand dunes and comprises over 5,000 pairs (Marchant, 1951). In the middle of April, 1955, nests in several areas of the colony were marked with numbers on small wooden sticks and inspected twice or three times daily until 6th May. Later, some of the nests were checked at various intervals. When it was noted how many eggs were stolen by other gulls, the eggs were marked at these checks. First, second and third eggs of a clutch are referred to as a-, b- and c-egg.

Egg-laying

In this section a few figures are given concerning the clutch size and the laying pattern as well as the seasonal and daily distribution of egg-laying in a Black-headed gull colony. For the Herring, Lesser Black-backed and Common gull (*Larus canus*) Paludan (1951) and Barth (1955) have provided similar information. After completion of my work a short paper of Goodbody (1955) on the breeding of the Black-headed gull came to my notice.

Seasonal Distribution

Darling (1938) tried to show that large colonies of gulls, and possibly of other birds, start laying earlier and lay their eggs within fewer days than do small colonies, and suggested that the date of laying depends partly on the amount of stimulation a gull receives from its neighbours' display. This has been called the "Fraser Darling effect." In a very large colony the situation appears to be more complex: Goethe (1937) found that different parts of a big Herring gull colony began laying at different times. Darling concluded from this that Goethe's colony probably consisted of a number of socially discrete sub-colonies and he suggested that these might show sequences of egg-laying similar to those which he claimed to have found for more isolated colonies.

While recording the dates of egg-laying at a large number of nests for the experiments referred to later (p. 155) some data were collected which have a bearing on Darling's suggestion about egg-laying in parts of a big colony of gulls.

Meanwhile, Darling's main points have been checked by Goodbody (1955) and by Coulson & White (1956). Goodbody's data suggest that the dates of laying of the first clutch may be more scattered in small Black-headed gull colonies (less than 50 pairs) than in bigger ones of over 100 pairs. It must, however, be noted that these figures are based only on clutches which later hatched. Bias caused by robbing is therefore not excluded (see p. 152). Goodbody also observed that the gulls of the larger colony started laying earlier on the average, but it appears that some abnormal factor was delaying the onset of breeding in the smaller colony. He thinks therefore that his results neither support nor refute these of Darling. Coulson & White (1956) conclude that there is no evidence for a Fraser Darling effect and suggest from their results that small colonies start laying later because they have a larger proportion of young birds than large colonies.

Groups of nests in various places were marked in the colony on 14th April and checked regularly. Group 1 (see Table I) consisted of 15 marked nests which were together on a steep hill, more than 60 yards away from any other group. Group 2 (of 31 marked and about 30 unmarked nests) was on a flat hill near the shore, more than 40 yards away from the next group. Groups 3 and 4 (with 61 and 70 marked and 10 and 30 unmarked nests respectively) were on two adjoining hills, separate from any bigger group by more than 100 yards. Since they were so close together they possibly formed one sub-colony. Group 5 consisted of 58 marked nests in a part of a large colony

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Table I. Seasonal Distribution of Egg-laying in Discrete Parts of Different Size of a large Black-headed Gull Colony

Group	Number of nests checked	Number of clutches found	Total number of nests in group	Average laying date (median)*	Period (days) in which 80% clutches were begun
1	15	12	15	23 April	6
2	31	28	c.60	25 „	11
3	61	44	c.70	26 „	11
4	70	44	c.100	24 „	15
(3 + 4)	131	88	c.170	25 „	14
5	58	33	700—1000	25 „	11
round hides	60	35	—	—	—
Whole colony	295	196	c.5000	25 „	13

*Date before and after which 50% of the clutches were begun

group of between 700 and 1,000 nests. Sixty more nests were marked and checked regularly around the hides. In all areas more nests were built as the season advanced, but these are not counted here.

Eggs were laid until the middle of June, but it became more and more improbable that these were in fact first clutches since some second clutches were found at the beginning of May (p. 156). As the interest was in first clutches only, the recording of egg-laying ceased after May 6th and second clutches laid before this time were not counted; but second clutches laid in a newly acquired nest (p. 157) may not have been recognised as such.

In 99 of the 295 marked nests no egg was found between 14th April and 6th May. They may have been nests built by unmated males (many such males were seen building during April and May) or the second nests of pairs which laid in the other one, or the eggs may have been robbed before they were seen (p. 152).

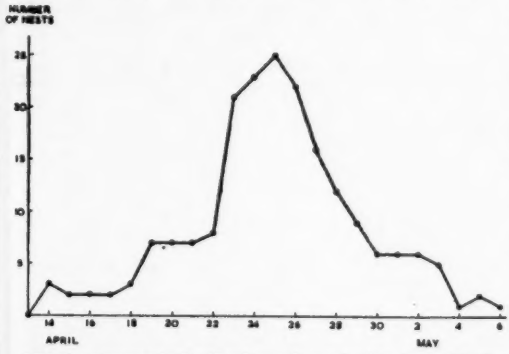

Fig. 1. Seasonal distribution of egg-laying in a Black-headed gull colony (Ravenglass, Cumberland). The dates are for the first egg found in 196 marked nests.

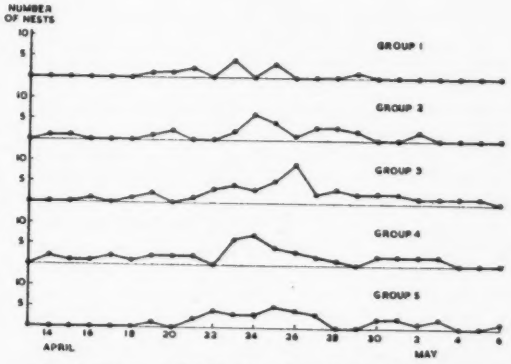

Fig. 2. Seasonal distribution of egg-laying in five groups of nests in the Black-headed gull colony in Ravenglass. The dates are for the first egg found in the marked nests of the different groups. See text.

Fig. 1 gives the seasonal distribution of egg-laying in the remaining 196 nests taken together. The curve shows a rather wide scatter over a longer period. There are twelve days between the onset and peak of laying, and in the first week only 13 per cent. of the 196 pairs had started laying.

This large scatter of egg-laying could be due to gulls in the different groups of the colony laying at different times, as Goethe (1937) found. From Fig. 2, which shows the distribution of egg-laying in the different groups, it will, however, be seen that this is not the case: all groups have their peak of laying between 23rd and 26th of April. In this interval are also the medians of their curves (see Table I).

However, many of these groups have a scatter of egg-laying no less pronounced than the whole colony, as judged from these groups taken together. This is measured by the period in which 80 per cent. of the clutches were begun, excluding thus the days on which the first and the last 10 per cent. of the clutches were laid. This measure is a more reliable guide for the scatter than the time between the laying of the first and the last clutch which would depend on two clutches only. From Table I it will be seen that this period varies between 6 and 15 days for the different groups and that it was 13 days for all the groups together. The wide seasonal distribution of egg-laying of the colony as a whole is thus mainly due to the wide scatter of egg-laying in each single group.

These groups varied in size, consisting of 15, 60, 70, 100 and 700-1,000 nests approximately (Table I). However, size and scatter of egg-laying (as measured by the "80 per cent.-interval") of a group are not correlated. (If log size and scatter are compared a *positive* correlation co-efficient of $r=0.54$ is obtained, which is, however, not significantly different from zero). Nor is the size of a group correlated with its average date of laying (as measured by the median). Darling's suggestion concerning the sequence of egg-laying in separate parts of a big colony was thus not verified.

Now it appears that even if the gulls influence the dates of laying of their neighbours (which was Darling's real concern) the effect this would have on the distribution of egg-laying in a larger group must be disturbed considerably by the constant arrival of new-comers. When observing gulls from a hide it was possible to recognize individuals by their wingtip patterns. But during April one could not stay away for more than three days without finding that many new-comers had replaced familiar individuals. Such new-comers either took over a territory which another pair had left (e.g. after it lost its eggs or after it had been chased away by its more aggressive neighbours) or they claimed ground at the boundaries of other territories which the rightful owners finally conceded. This had the effect that on a given area of the colony more and more birds began to breed as the season advanced. Obviously, these birds could not all be in phase.

On the other hand there is another way in which the colony "ensures" a synchronisation of the breeding activity of its members: Early in the season, when only a few gulls have laid, the others frequently try to take and eat these eggs. This was seen many times from the hide. Very few early layers hatched their first clutch successfully: most laid a second clutch.

A few figures substantiate this (Table II). From 39 pairs which laid between 14th and 21st April, i.e. before the mass-laying had begun, nearly half were robbed of all their eggs; only two clutches hatched without loss. This was certainly quite different with clutches laid at a later date. This was not systematically checked, but to judge from a few pairs which were studied more intensely, of clutches laid between 25th and 30th April (Table II) only one out of 12 was robbed of all its eggs.

Another way of measuring the amount of robbing was to count how many eggs were missing in a nest seven days after the first egg had been laid (Table III). However, some difficulties arose: in a few nests only two eggs were found. This could mean either that the bird laid only two eggs or that one was robbed;

Table II. Hatching Success of Three-egg Clutches laid at Various Times in the Breeding Season

Date of laying of a-egg	All eggs hatch	Two eggs hatch	One egg hatches	No egg hatches	Total of clutches inspected	% eggs hatched
14-15 April				5	5	0
16-17 „	1	1	6	3	11	33
18-19 „			3	6	9	11
20-21 „	1	2	7	4	14	33
For whole period	2	3	16	18	39	24
25-26 „	3	1			4	92
27-28 „	3	1			4	92
29-30 „	2	1		1	4	66
For whole period	8	3	0	1	12	83

Table III. Robbing of Eggs at Different Times in the Season Within a Week of the Laying of the a-egg

Date of laying of a-egg	No egg robbed	One egg robbed	Two eggs robbed	Full clutch robbed	Total of clutches inspected	% clutches not affected by robbing	% full clutches robbed
April 14—18	3	5	2	6	16	18	37
19—22	13	6	2	5	26	50	19
23—26	25	12	1	4	42	59	10
27—30	11	5	0	1	17	65	6

such nests were omitted from the list. In nine other nests only one egg was seen; as it is unlikely that in so many cases only one egg was laid (p. 154) at least one egg must have been robbed, possibly two; such nests are counted under "one egg robbed." In 13 nests only one egg was recorded which at a later date disappeared; here again it is not clear how many eggs were laid and robbed but the effect was probably the same as if three eggs had been destroyed from a full clutch, i.e. the birds left and were forced to lay another clutch later; these cases are included under "full clutch robbed."*

In spite of these drawbacks Table III seems to show clearly that birds laying between 23rd and 26th April (at the height of laying) or later are less likely to be robbed of their eggs within seven days than birds laying right at the beginning of the season.

Daily Distribution

Paludan (1951) found in 7 clutches of *Larus argentatus* and *Larus fuscus* that the first egg tended to be laid late in the morning or early in the afternoon, while b- and c-eggs were laid between the evening and the following morning. Barth (1955) did not find this in 129 eggs of *Larus canus*: a-eggs were laid at practically any time of the day, and the b- and c-eggs were somewhat concentrated between 12.00 and 17.00 hours. But Barth mentions that "the small number recorded around midnight may be due to fewer observations between 22.00 and 05.00 hours"; this makes it rather difficult to use his figures. More data are needed for both Herring and Common gulls before the issue can be settled.

*According to experimental results (p. 155) it is possible that a number of pairs might have deserted as soon as the first egg had been robbed. It is not clear what happens with the *b*- and *c*- eggs in such cases.

An attempt was made to get some idea of the daily distribution of egg-laying in the Black-headed gull by visiting 138 nests two or three times a day and recording the eggs laid. As the nests to be inspected were marked before there was an egg in them, the figures obtained should represent a fair sample of the colony; this eliminates the bias encountered in Barth's work towards eggs laid at a particular time of day.

On the average slightly more a-eggs were laid during the "day" (i.e. from about 07.00-19.00 hours) than during the "night" (i.e. from about 19.00-07.00 hours). However, the difference is not significant ($P > 0.6$). For the b-eggs there was a slight difference between the day and night values in the first six days of recording ($P = 0.05$), but the values are rather small and may have been distorted by robbing. In the second six-day period the figures for day and night are not significantly different, and since there were more clutches in this period and robbing was less this conclusion is more reliable. For c-eggs there is no difference between day and night.

The numbers of a-, b- and c-eggs laid in the "morning" (i.e. between about 07.00 and 13.00 hours) and in the "afternoon" (i.e. between about 13.00 and 19.00 hours) do not significantly differ. However, these last results are based on only 47 eggs since we only visited the colony a few times at midday.

To sum up, the Black-headed gull shows no tendency to lay its eggs at one time of day rather than at another.

Clutch Size

The Black-headed gull is generally believed to lay 3 eggs and less often 2 eggs in its first clutch, whereas the second clutch is supposed to consist more often of 2 than of 3 eggs (Noll, 1931; Witherby, *et. al.*, 1938-41).

The figures collected confirm this. Out of 184 early, presumably first, clutches inspected, 3 eggs were found in 129 nests (70 per cent.). In 26 nests (14 per cent.) we only found 2 eggs and in 29 nests (16 per cent.) only one. However, since half of the nests with one egg, and a third of the 2-egg nests were later deserted, it is likely that many of these had been robbed before we inspected them. I think it, therefore, probable that much more than 70 per cent. of the birds laid in fact 3 eggs.

For second layings the percentage of 2-egg clutches may be higher. In 3 out of seven nests only two eggs were found at a time when robbing was rare. For clutch sizes of one-year-old birds see p. 160.

Barth (1955) states that one in every 5 nests of the Common gull has only two eggs. He does not say how he arrived at this and whether the possibility of robbing is excluded. According to Paludan (1951) two-egg clutches occur in less than one per cent. of undisturbed first clutches of the Herring gull. He found more 2-egg clutches in the Lesser Black-backed gull but doubts whether the difference is real. Twice he found four eggs in one nest which he considered to be laid by one ♀.

Laying Pattern

For the experiments on egg-laying it was necessary to know the laying pattern, i.e. the intervals between the laying of any two successive eggs in the clutch. Laying patterns have been recorded by various authors for the Herring gull and the Lesser Black-backed gull (see Paludan, 1951) and by Barth (1955) for the Common gull. It was therefore interesting to compare their results with mine and to see whether the laying pattern differs between these species.

As the colony was inspected only two or three times a day the margin of error for the single observation is $\pm\frac{1}{2}$ day. In 8 clutches a- and b-eggs were laid within less than $1\frac{1}{2}$ days. Fig. 3 gives the frequency of different laying patterns of 69 nests. The most common ones are drawn in heavy line. Fig. 4 shows the distribution of the length of the intervals between the laying of a- and b-eggs, b- and c-eggs, and a- and c-eggs. The mean length of the interval between a- and b-eggs is not significantly different from that of the interval between b- and c-egg (P=0.06).

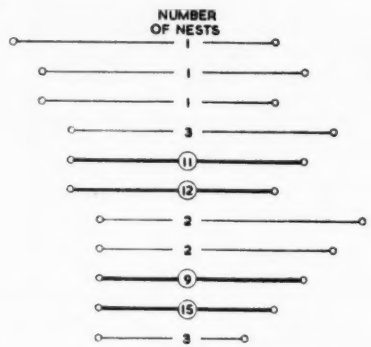

Fig. 3. Laying patterns of 69 nests. Most frequent ones are drawn in heavy line.

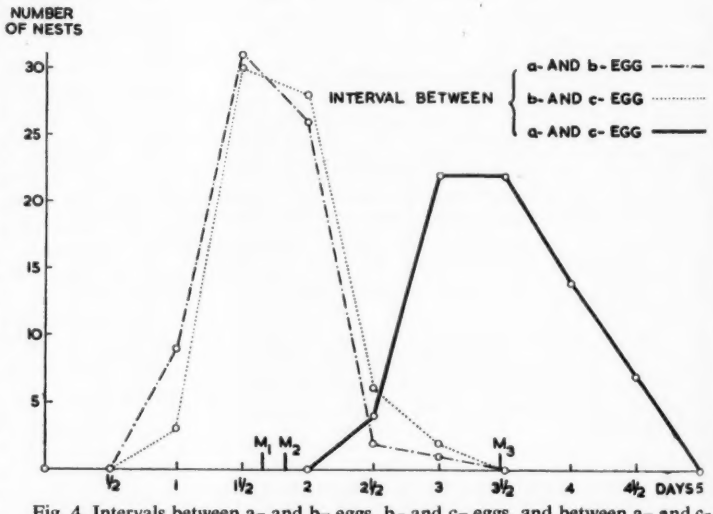

Fig. 4. Intervals between a– and b– eggs, b– and c– eggs, and between a– and c– eggs in 69 nests. M1, M2, M3: the mean length of these three intervals.

In order to compare the variation of the laying pattern for the various gull species, mean and standard deviation of the mean were calculated from the figures of Paludan and Barth. Moreover, it seemed desirable to estimate the influence of the observational error on the error of the mean, because there were so few classes in these samples (Paludan has only 3) and the margin of error of the single observation (± 1 day in Paludan's case) was equal to twice the class width.

Even when all this is taken into account the mean intervals between the laying of a- and b-eggs in the Black-headed gull (40.32 ± 1.14 hours) and in the Common gull (47.77 ± 0.93 hours) are significantly different ($P = 0.01$). So are the intervals for Black-headed gull and Herring gull (48.36 ± 1.09 hours) at the 5 per cent. level. The mean interval between laying of a- and c-eggs of the Black-headed gull (83.66 ± 1.55 hours) is significantly different ($P = 0.01$) from the mean intervals in the Common gull (93.50 ± 1.44 hours) and the Herring gull (98.54 ± 1.71 hours). These figures would suggest that the Black-headed gull lays its clutch on the average in a shorter time than do Common and Herring gull.

Egg-laying Experiments

Removal of Eggs

In an extensive series of experiments Paludan (1951) showed that the Herring gull and the Lesser Black-backed gull are not determinate layers as was hitherto claimed (Stresemann, 1927-34; Davis, 1942; Tinbergen, 1951*). Like Salomonsen (1939) he induced gulls to lay d-, e- and more eggs by taking each egg as soon as it was laid. In order to see whether his findings hold good for the Black-headed gull also the following experiments were carried out.

In the first series of experiments the a-egg was removed from 23 nests within 12 hours of laying. Just over half of the nests were deserted; in 8 nests 3 more eggs were laid, the d-eggs 2 days after the c-eggs in 6 cases, and 3½ days after in two cases. Of the remaining 3 nests one contained one egg only, the others had b- and c-eggs. Eggs may have been robbed in these cases.

*Both Davis and Tinbergen removed eggs from Herring gull nests. Davis found a fourth egg in a number of cases, but interpreted them as artefacts, e.g. as due to interference by other pairs, etc. Tinbergen never found a *d*-egg, but he does not say how many experiments he carried out.

In 12 nests we removed both a- and b-eggs, less than 12 hours after each was laid. Five nests were deserted after the removal of the b-egg. In 5 nests we found d- and e-eggs. The interval between the d- and the e-egg was 2-3 days. Two cases were doubtful.

In 6 nests the a-, b- and c-eggs were removed as soon as they were laid, or at least not more than 12 hours later. In 2 nests three more eggs were laid on alternate days; one nest had d- and e-eggs only; this ♀ laid all her eggs in a much slower rhythm, i.e. on the 19th, 22nd, 25th, 27th and 30th of April. In one nest a d-egg only was found, and 2 nests were deserted.

By removing 5 eggs as each was laid 7 eggs were obtained from one nest, laid on alternate days. That no 8th egg was laid might be due to the 5th egg being left a little too long in the nest before it was removed (p. 156).

From these experiments (summarized in Table IV, A) it is clear that the Black-headed gull is not a determinate layer any more than the Herring gull. Under suitable circumstances it will add as many eggs as have been removed (*protracted laying*) bringing the number of eggs in the nest up to three again. Of 42 nests robbed 19 were deserted and 15 had three eggs again at the end.

In the light of these results it seems worth while to reconsider other cases of alleged determinate laying. It may well be that protracted laying has been overlooked in other species, too. As will be seen later the eggs may be left in the nest for a limited period only before being removed for protracted laying to occur, and this critical period might be even shorter in other species. With this possibility in mind, Poulsen (1953) carefully rechecked the egg-laying of pigeons but confirmed previous results that it could not be protracted.

How is the clutch size in an indeterminate layer controlled? The most obvious hypothesis would be that the birds stop laying when they perceive, e.g. see or feel, a complete clutch. Mechanisms working on this line have been suggested: e.g. egg-laying might stop when all brood-patches were in contact with eggs (Stresemann, 1937-34); or a visual IRM for the sight of the full clutch might be involved (see Koehler, 1940).

However, for the Herring gull Paludan (1951) was able to rule out this hypothesis experimentally. He allowed the gulls to brood on the a-egg but removed the c-egg, or the c- and b-eggs as soon as they were laid. None of

Table IV. Egg-laying Experiments. Removal of eggs during and after laying, d, e, f, g: d-egg, e-egg, f-egg, g-egg

Number of eggs left in nest‡	Number of experiments	No extra eggs laid	Protracted laying up to				Repeat laying	Deserted	Doubtful
			d	e	f	g			
A.									
0. 1. 2.	23	3	8					12	
0. 0. 1.	12			5				5	2
0. 0. 0	6		1	1	2			2	
0. 0. 0. 0. 0	1					1			
B.									
1. 1. 2	10	10							
1. 1. 1	2	2							
C.									
1. 0. 1	11	2	5					4	
D.									
1. 2. 0	10						2*	8	
(1 clutch robbed)	15						6†	7	2

*After 9-10 and 10-12 days.
†After 8-10 and 7-11 and 9-13 days and 3 times after 8 days.
‡The Code indicates how many eggs were left in the nest at the end of the examination after each egg was laid. Thus in 0. 1. 2 no egg was there after the a-egg had been removed; when the gull had laid the b-egg, it was now sitting on one, after laying the c-egg it possessed two, etc. (after Paludan, 1951).

these birds laid a d-egg, in spite of the fact that they saw and felt an incomplete clutch only. This was confirmed also for the Black-headed gull which similarly incubates from the first egg onwards (Table IV, B.).

The size of the clutch when the bird stopped laying was thus not involved in the control of egg-laying. Nor was it at any other time: Paludan added eggs to the clutch as soon as the first egg had been laid, without it having any effect on the laying process. The only thing correlated with laying in his and our experiments appears to be the bird's brooding: once it is brooding it will lay only two eggs more; the brooding must in some way be connected with the cessation of egg-laying. (It cannot be decided at the moment whether the brooding activity as such, itself released by the presence of eggs, might inhibit egg-laying or whether the prolonged stimulation of a brood-patch by an egg might do this directly).

There are, however, some experiments on the effect of the *duration* of brooding on egg-laying. How *long* must the bird brood for the d-egg not to appear? This was investigated by removing the eggs in the middle and towards the end of the normal laying period.

In 11 nests both a- and b-eggs were removed together less than 18 hours after the b-egg was laid; thus the birds which had brooded till then could not brood further until they had laid the c-egg (Table IV, C). All the same, 5 females laid a d-egg, two laid and brooded a c-egg only and four deserted. The next series of experiments (Table IV, D) shows that removing the eggs after the c-egg has been laid never induced the gulls to lay a d-egg. In fact all 25 pairs left.*

Thus 2-2½ days' brooding was not always enough to stop a d-egg but 4 days' brooding, during the whole interval between the laying of a- and c-egg always was.

In the Herring gull Paludan (1951) did a number of similar experiments which suggest that the d-egg is laid if, by removing the eggs in the time between the laying of the a- and c-egg, no eggs are in the nest for at least twenty-four hours, whereas if the nest is empty for a shorter time the d-egg is suppressed.

Of the 25 pairs which left after they lost their full clutch (Table IV, D) 10 pairs were known individually. Two of these were occasionally seen on their territory afterwards and started to lay a full second clutch 9-10 and 10-12 days later. Such *repeat laying* may have occurred also in 6 other nests where the first clutch was

*The possibility that they might have laid a *d*-egg elsewhere is remote if the evidence on p. 159 is taken into consideration.

robbed by other gulls. In these nests another clutch was found 8-13 days after the previous one was destroyed. It may well be that this was from the same female although in these cases we have no proof of this.

In fact it was repeatedly seen that a few hours after a certain pair had deserted its nest another pair occupied it for good and sometimes laid eggs within 3 or 4 days. Once an egg was found one day after a new pair had taken possession of a deserted nest. This however seems to be rare. Nevertheless, it has to be taken into consideration for some cases of alleged protracted laying, especially when the interval between any two eggs is more than two days. However, it cannot account for all the cases, as some experiments were carried out with birds which were recognised individually. Only twice was it believed that 2 females laid in the same nest, since the eggs found were of strikingly different colour. Moreover, in one of them the fourth egg appeared 12-18 hours after the c-egg, though no egg had been lost.

These findings do not support Salomonsen's (1939) assertion "that on account of this strong sense of territory in the (Herring) gulls it is possible to conclude that a pair will stick to the same restricted *locality* even if the nest has been robbed and if a new egg is found in such a nest it must belong to the original pair whose eggs have been removed." Herring gulls of course may be different from Black-headed gulls in this respect. It is true, in the Black-headed gull too, that many nest-owners which have lost their clutch return after some days to the vicinity of the nest. But many will then build a new nest not necessarily within the limits of their old territory. We saw a pair occupy a new territory more than 10 yards away, separated from the old place by territories of neighbours. For these reasons great care must be exercised when interpreting results of protracted and repeat laying by birds which are not individually known. Some of the results presented in this paper as well as those of Salomonsen (1939) and Paludan (1951) may not be reliable.

Presentation of Eggs to Gulls which had not Laid

Whereas adding eggs to a nest which already contained an egg never influenced egg-laying in Paludan's (1951) experiments, he succeeded in a number of birds in suppressing the last egg by putting eggs which they brooded in their nests a number of days before they had begun to lay. In two cases egg-laying might have been suppressed altogether but the evidence is not conclusive. As Paludan (1951) points out, it is impossible to follow a systematic plan in these experiments as it cannot be known beforehand when the bird is going to lay.

Artificial eggs were put into 60 nests belonging to pairs which had not had eggs previously in the season. Their behaviour was observed daily from a hide for 2-4 hours. Unfortunately, only in a few cases was it possible to distinguish between the two mates of a pair. The nests were inspected 2 or 3 times a day for eggs. The "eggs" used were wooden models, painted to resemble Black-headed gull eggs. It was never noticed that gulls treated them differently from real ones with one exception where a bird first tried to break an egg (and would have done so if it had been a real one) but then gave it up and instead sat on it (R. Weidmann, in preparation).

In 26 nests the eggs were never incubated; after some days, therefore, most of them were removed. Some were left for 3 weeks and in some of these nests a bird was seen to sit once or twice and never again, in others no bird was ever seen near; the nests deteriorated after a while, because the owners had left. No eggs were laid in any of these nests.

In all the other 34 nests a bird was seen sitting regularly either from the day on which the eggs were given or within a few days (Table V). In a few nests we observed that at first only the ♂ was sitting, in others both birds sat from the beginning and in many other cases we could not decide. After some days, however, it was known that both mates took part in brooding as their nest-reliefs were observed.

Of the 34 pairs 13 never laid an egg. Two of them stopped sitting after 10 and 11 days and left, probably because they were disturbed when an attempt was made to ring a nearby bird. The others sat for a long time, some for over two months. As the exact date of their desertion is not known, the total brooding time is calculated from the date we last observed them. For some pairs this was only a few weeks before the colony left the breeding area entirely on 11th July. Kirkman (1940) saw Black-headed gulls incubate for 75 days.

In 4 nests one egg was laid, in 13 nests two eggs were found and in 4 nests three. Table V shows how many days the eggs were brooded before the ♀ laid the a-egg.

From this the following conclusion may be drawn: one day's sitting before the laying of the a-egg was not enough to suppress the c-egg.

Table V. Egg-laying Experiments. Presentation of eggs to gulls which had not yet laid. Birds which did not sit omitted.

(*a*) Birds which subsequently did not lay :

nest No.	Number of days of commencement of brooding after eggs were presented*	Total brooding time (in days)
201	1	11
203	4	>39
209	1	>71
250	1	>62
258	1	>61
260	1	>63
4	4	>66
214	2	>25
249	2	>39
259	5	10
359	2	>36
353	3	>54
252	3	>38

*With exception of the last 2 nests which were presented with eggs on 6th May, all eggs were presented between April 14th and 19th.

(*b*) Birds which did lay :

	Nest No.	Number of days before laying of a-egg: when eggs were presented*	when pair began brooding†	when female was first seen brooding‡
one egg laid	208	9	7	5
	248	6	5–6	
	201	?	5–7	
	318	5	5	5
two eggs laid	202	14	g	6
	246	9	8–9	
	220	8	7–8	
	347	7	7	
	331	7	6	6
	320	8	6	6
	257	10	6	6
	211	6	2–6	
	219	4	4	
	319	4	4	4
	juv.	6	4	4
	105	3	3	
	254	3	2–3	
three eggs laid	U	1	1	1
	X	1	1	
	YY	1	0–1	
	253	1	1	

*All eggs were presented between April 14th and 25th.
†Possibly only one of the pair was brooding.
‡The female may have been brooding before that time.

In one case 2-3 days' sitting had this result; in some cases, however, the ♀ was seen brooding as early as 6 days before, and still it laid 2 eggs. Unfortunately, it is not possible to be sure how persistently the ♀ brooded. Paludan (1951) comments on this possible error of over-estimating the time the ♀ has sat on the eggs when the female's activity is not directly observed. That fewer days' persistent sitting are enough to suppress the c-egg is the more probable since in 4 cases 5-7 days were enough to prevent all but one egg from being laid. It is planned to check this in the near future. Only by extrapolation can one estimate the least number of days the ♀ has to sit to stop her laying any egg, This is probably 7-8 days before the a-egg would have been laid. That females may be ready to sit two weeks before laying was shown by R. Weidmann (in preparation). She put wooden eggs in several nests and watched the gull's behaviour for 2½ hours. Then the eggs were removed and the number of days was recorded after which the gulls laid their own eggs.

Inspection of Ovaries and Discussion of the Egg-laying Mechanism

In order to gain more understanding of the egg-laying mechanism and to repeat Paludan's observations, 5 females were killed at various times in the egg-laying cycle and their ovaries inspected.

A bird killed on April 8th before egg-laying had started in the colony had no follicles with a diameter bigger than 4 mm; only 4 eggs were of this size, 8 eggs had a diameter bigger than 3 mm, and more than 20 eggs were smaller. The biggest follicles were attached to the ovary with a thin stalk only. Some of them were slightly yellowish, but clearly not much yolk could have been deposited.

On 22nd April another bird was killed which had its first egg in the oviduct. It was so large that it flattened under its own weight, probably it would have been laid within 24 hours. In the ovary were 4 more eggs larger than the others and different in colour. Especially noteworthy were the two smaller ones which had diameters of 8 and 6 mm. Both had long stalks and were of a distinct orange-yellow colour, showing that yolk had been deposited for some time. None of the other eggs had developed beyond the stages already found in the previous bird. It is difficult to say when the two smallest of the orange coloured eggs had

started the final deposition of yolk; there may not be a sharp limit; the difference in colour might be an indication not of presence or absence of yolk but of the *amount* of yolk deposited. Birds killed some days *before* laying might give an answer.

From the results discussed previously (p. 155) it is known that a d-egg might have been laid 7 days later, i.e. 6 days after the a-egg. It seems reasonable to assume that the two small, yolky eggs were the d- and e-eggs. So the course of growth of the d-egg can be roughly extrapolated from the measurements of the c-, b- and a-egg at the time of death: Two days later the d-egg would have been as large as the c-egg at the time of death, etc. This gives the following growth curve (Fig. 5). When one considers

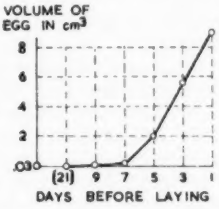

Fig. 5. Growth curve of egg (yolk) in the ovary extrapolated from the sizes of 5 eggs at different stages of development in a killed Black-headed gull.

how little progress the d-egg had made up to this moment (comparing its size with the size of the e-egg and the size of the biggest reserve eggs), the sudden speed of growth during the last few days before laying is striking. The term "final phase of yolk deposition" (Stieve, cited in Paludan, 1951) thus has a real meaning even if it should not be possible to mark its beginning sharply.

On April 26th a ♀ sitting on the a-egg was caught. Besides the calyx of the a-egg, a broken flat sac, b-, c- and d-eggs were found in the ovary; unfortunately c- and d-eggs were damaged during dissection so that no exact measurements can be given. The d-egg was yolky and showed no signs of degeneration. No other egg was different from the mass of reserve eggs.

On 7th May a ♀ was killed 6-18 hours after it had laid its b-egg. The c-egg was in the oviduct. A d-egg which had clearly started to degenerate was found in the ovary. A little yolk was still visible, but the surface was shrivelled up and had partly lost its yellow colour. (For a discussion see p. 159). No e-egg was present.

On May 28th a ♀ in the first summer plumage (p. 160) was caught 10-24 hours after laying the c-egg. Three calyces were found; one, presumably from the a-egg was rather smaller than the others. There were also two yolky eggs; the bigger one was a degenerating flabby sac, partly pinkish, partly orange in colour; the smaller one showed no signs of degeneration. The other eggs were of the same size and appearance as those found in the first ♀ killed.

In general, these observations are well in agreement with the description Paludan (1951) had given for the Herring gull. In all examined specimens a d-egg (and sometimes an e-egg) had entered the phase of rapid growth which ceased in the two specimens killed after the b-egg was laid.

Some remarks may be added.

The gull killed on 7th May had a d-egg in advanced degeneration though at the most the b-egg was laid 18 hours before. Obviously it could not have laid a fourth egg after two days, if its eggs had been removed at this time. This may mean that the "sensitive period" is shorter in the Black-headed gull than in the Herring gull where Paludan asserts that it lasts 24 hours after the b-egg has been laid. On the other hand, it is possible that there is some individual variation as to the time when the d-egg degenerates. On p. 156 it has been shown that at least some females lay a d-egg when their eggs are removed right after laying of the b-egg. Such individual variation might among other things be due to the possibility that some females brood for longer periods than others.

As Paludan (1951) pointed out, the influence of sitting on eggs affects the follicles differently. The c-egg is laid after the gull has sat on its a-egg four days or longer. Obviously then, there is a stage of development after which an egg will grow to maturity and ovulate whatever the gull's activity. Before this stage an egg degenerates when the gull is brooding. This limits the number of eggs to be laid after the gull has begun to sit. Another less well defined boundary is given by the beginning of the final rapid growth. As seems likely from Paludan's (1951), Salomonsen's (1939) and from the writer's own experiments a gull may lay 7 eggs in series and possibly more. This means more and more eggs pass this limit the longer the gull is prevented from incubating after it has laid eggs. The links in the chain of factors controlling this is not yet known, nor how the degeneration

of eggs in this phase is brought about when the gull is sitting.

The last ovary dissected was of a gull in the characteristic first summer plumage, which according to general belief (Witherby *et al.* 1938-41) is typical for one year old birds*). For some time it had been thought that Black-headed gulls could not breed, before they have assumed adult plumage, (Dwight, 1925). However, Noll (1931) and Haverschmidt (1931) saw females in the first summer plumage brooding and v.Oordt (1934) describes that the ovary of one such ♀ was active. The present investigation confirms his conclusion: Apart from the ♀ mentioned it was found that several other females in this plumage had laid two or three eggs. This does not quite agree with Noll who never found 3 eggs in the nests of one-year-old birds. Males in this plumage were seen to court females and defend territories but out of more than 30 individuals observed none stayed in the vicinity and bred.

Summary

Two hundred and ninety-five nests of a Black-headed gull colony were inspected for eggs once, twice or three times daily from 14th April till 6th May, and at irregular intervals later. In 196 nests first clutches appeared over a period of more than three weeks. In the first week only 13 per cent. of the birds started laying. Darling's (1938) suggestion that discrete parts of a big colony behave as he thought isolated colonies did, could not be verified. Slightly more a-, b- and c-eggs are laid during the day than during the night but the differences are not significant. No significant difference was found for the number of eggs laid in the afternoon and in the morning. Of 184 clutches 70 per cent. consisted of 3 eggs. This figure is almost certainly too small, because it does not include the clutches which had been robbed before they were inspected. The most common interval between the laying of successive eggs of a clutch is 1½-2 days. The mean interval between the laying of the a- and b-eggs is not significantly different from the mean interval between the b- and c-eggs. The Black-headed gull lays its clutch in a shorter time than do Common and Herring gulls.

If the a-egg was removed within 12 hours after it was laid the ♀ laid a d-egg 2 days after the c-egg. If both a- and b-eggs or all 3 eggs were removed immediately after each was laid protracted laying occurred in a number of cases. In one nest 7 eggs were obtained from one ♀. Therefore, the Black-headed gull also is an indeterminate layer as Salomonsen (1939) and Paludan (1951) proved for the Herring gull and the Lesser Black-backed gull. Reducing the number of eggs had no effect on egg-laying if one egg was left in the nest. It is thus not the size of the clutch but the gull's brooding which causes the cessation of egg-laying. Removing both eggs immediately after the b-egg was laid caused protracted laying in a number of cases. If, however, all eggs were removed after the c-egg was found no further egg was laid immediately but a full second clutch appeared after 8-13 days.

By adding eggs several days before the gulls laid it was possible to suppress egg-laying completely or partially: 13 pairs never laid though many brooded our wooden eggs for 2 months. In 4 nests one egg was laid after 5-7 days' sitting, in 13 nests we found 2 eggs and in 4 nests where the birds had only sat for one day all 3 eggs appeared.

Five ovaries were inspected at various times during the egg-laying cycle. Around the time the first egg is laid, the second and third are successively smaller and a tiny fourth follicle was found, apart from the still smaller reserve eggs. In two birds killed after the b-egg had been laid this d-egg was degenerating. It is concluded, as it was for the Herring gull (Paludan, 1951), that incubating has an inhibitory influence on the growth of follicles and causes them to degenerate as long as they have not reached a certain stage of maturity. This limits the number of eggs to be laid after the gull has begun to sit.

Acknowledgments

The work was undertaken as part of a comparative study of gull behaviour supervised by Dr. N. Tinbergen and supported by the Nuffield Foundation. I should like to thank Professor A. C. Hardy, F.R.S., for allowing me to work in his department and Dr. Tinbergen for his help and interest in the work. I am very grateful to Major G. Pennington, the Nature Conservancy and Carlisle County Council for permission to live and work in the gullery at Ravenglass, and to Mr. J. Farran, the Head Warden, for help of various kinds. Finally, I should like to thank Miss O. Razumovsky, Mr. A. Zahavi, and my wife for assistance in

*As far as is known this has never been checked with ringed birds,

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CORRESPONDENCE

The Sources of Some Ethological Notions

SIR,

At a recent Conference on Group Processes (1955) a number of notions current, or recently current, in comparative ethology were considered. As I am wrongly credited with one of them, it seems worth while tracing their history, if not to their origins, then some way back into the past.

On p. 182 Dr. K. Z. Lorenz makes the following statements regarding the differences in the threshold of stimulation needed to evoke instinctive movements. "The first assumption is, in both cases, that 'something' is accumulated during the rest period of the activity which is destroyed during its performance. Holst thought that this 'something' might be humoral, a theory which was independently proposed by J. B. S. Haldane at the symposium on instinct recently in Paris."

At that symposium I made no claim for originality in this matter. I pointed out that the notion of a reservoir which was exhausted by activity and then filled up again, put forward by Lorenz (1950, and earlier) was due to McDougall (1923). If I remember I first met with it in his lectures in 1913.

McDougall, in the book cited, devoted three pages (107-109) to this hypothesis. He discussed whether it was better to postulate one reservoir or a separate reservoir for each instinct. He finally produced the following "mechanical analogy." "Each instinct is represented by (1) a chamber within which a process of fermentation or other chemical change liberates a gas, which accumulates under pressure. The several chambers communicate with one another by fine channels through which the gas can pass against considerable friction, when the pressure in any two chambers is different. (2) Each chamber has an outlet which branches into a complex system of pipes leading to a group of executive organs (nerves leading to muscles and glands). (3) This outlet is closed by a door or sluice-gate provided with a lock of more or less complex pattern peculiar to itself (in some cases it is a series of locks rather than a single one). This door is never quite gas-tight; gas leaks through, and leaks in larger quantity the higher its pressure in the chamber (appetite and the restlessness in which it is expressed). When the key is turned, the door swings open and the gas, issuing along the many channels, sets in action the various mechanisms to which it is led . . . The key is the sensory-pattern presented by the specific object of the instinct (e.g. the nightingale's song, the peacock's tail)." He continued that the analogy might be improved by replacing the locked door by a spring valve, actuated by a lever held back by a series of stops. "The complete depression of the lever and the fullest opening of the valve occur only when a certain combination of keys is struck; the striking of some of these keys will permit a partial depression of the lever." He was inclined to locate the sluice gates in the thalamus. McDougall clearly borrowed some of his ideas from Descartes, who located the sluice gates in the pineal gland.

Lorenz' (1950) model was very similar to McDougall's, but he did not admit communication between different reservoirs. McDougall postulated such communication to allow for what are now called displacement activities. Lorenz was evidently unaware of McDougall's priority. The works of Drees (1952) on jumping spiders suggests that it might be better to think in terms of several sluice-gates for one reservoir. Zupancic (1953) has further developed the theory, and thinks that the destruction of the substance stored in the reservoir yields the energy which starts nervous impulses. In particular carbon dioxide is destroyed by carbonic anhydrase in the respiratory centre. I must emphasise that McDougall, though a vitalist, did not regard this biochemical hypothesis as a metaphor. "We are naturally inclined" he wrote, "to suppose that it is a case of conversion of potential energy, stored in the tissues in chemical form, into the free or active form, kinetic or electric or what not; and probably this view is correct. And we may legitimately speculate on the sources, the seat of storing and liberation, and the mode of direction of the liberated active energy, in purely physiological terms."

A casual reader of this part of the Macy Foundation Discussion might think that Dr. Lorenz did not himself believe in the reservoir theory. However on p. 147 Dr. Lehrman suggested that "Dr. Lorenz's hydraulic models might be misleading," and added "The releasing mechanism is described as if it were a set of valves." To which Dr. Lorenz replied "That is exactly what it is."

The McDougall-Lorenz reservoir hypothesis was discussed for some fifteen pages, by which time it had become "Haldane's assumption." In Paris I illustrated it from the relation of carbon dioxide to the respiratory centre. A better example might have been the potassium in a nerve fibre. When an impulse passes along a fibre the membrane becomes permeable, potassium flows out, and sodium flows in. An important part, perhaps the essential part, of the recovery process is the activity of a "sodium pump" which reverses this process. It is probable, but not certain, that the same thing happens when the cell body of a neuron is stimulated. But I cannot regard an increase in the permeability of a cell membrane as being, in Dr. Lorenz' words "exactly" the opening of a valve. This is a metaphor. The accumulation of a substance may not be a metaphor.

I suggested, and still suggest, that McDougall and Lorenz were quite right in proposing that the readiness of a "centre" or small volume of the nervous system to produce nervous impulses depends on the concentration in it of some substance or substances. I think it unlikely that they are often as simple as carbon dioxide or potassium. They might for example be precursors of acetyl-choline, or the various neuron-stimulating compounds which have been found in different parts of the brain stem (v. Vogt, 1954) for example serotonin. It seems to me more likely that activity reduces the amount of such a substance than that it acts by "the reduction of tissue tension," as Lehrman (Group Processes, p. 190) suggested. I do not suppose that Professor von Holst has any more wish than I to deny McDougall's priority.

On pp. 181-182 of the same discussion Lorenz described the behaviour of a decapitated sea horse, whose spinal cord activates its dorsal fin. The passage which I quoted in the second paragraph continues as follows. "The second assumption is that the highest levels of brain function hold the continuous and spontaneous process under control under an inhibition which is removed only when the instinctive movement should be performed." Once again, this assumption is in no way novel. When I attended his lectures and demonstrations in 1920 and 1921, C. S. Sherrington made it as a matter of course. The most striking examples are "decerebrate rigidity," or decerebrate standing, which occurs in many mammals, and the intrauterine convulsions which are characteristic of anencephalic human embryos, in which the cerebrum is replaced by vascular tissue but much of the brain stem may be formed. As I pointed out in Paris, the notion of release of function by removal or injury of cephalad parts of the nervous system is due to Hughlings Jackson (1931). This is the date of posthumous publication of his collected papers. He developed the notion on the basis of human clinical studies in the nineteenth century.

It seems reasonable to suppose that the centres for instinctive activities of mammals are mostly situated in the brain stem, where Hess and others have located some of them. They are normally inhibited by impulses coming down from the cortex. And since their release often depends on the perception of fairly complicated visual or auditory patterns it is probable that "innate releasing mechanisms" (McDougall's "locks") are located in the cortex. This is not inconsistent with the fact that the early stages of an instinctive act often include complicated adjustments to the environment which involve the cortex as well as the brain-stem and thalamus. The final consummatory act can usually be carried out even when the cortex has been removed.

I think that Jackson's work affords powerful support to Lorenz' notion of "releasers" and gives a more concrete idea of the neurological processes involved than is to be found in some recent ethological writings. Certainly the phrase "release of function" is to be found in Jackson's writings, though it may well have earlier sources, and is in fact implicit in such words as "self-control."

On p. 190 Dr. Lorenz spoke of the reinforcement of instinctive processes by the consummatory act and in his concluding remarks (p. 288) said "Remember Wallace Craig's great discovery that the goal or end towards which the organism is striving, is not the survival value of its behaviour patterns, but the consummatory act itself." He might have added that the goal was not the pleasure which (by analogy with human experience) is associated with some consummatory acts. Aristotle, in his Ethics, defined the word *eudaimonia* (generally translated as happiness) as *energeia anempodistos*, which means an unimpeded endogenous activity. Precisely the same idea is found in the Indian Samkhya philosophy, almost certainly somewhat prior to Aristotle. For example in a section of the Bhagavad Gita which claims to expound this philosophy it is stated that the

wise man should work without troubling whether or not his work brings a reward. This doctrine is rather pompously called the doctrine of non-attachment. Craig certainly deserves credit for showing that pigeons act according to the principles laid down by moralists for men, but hardly for discovering these principles.

The ethological school has discovered many important facts, but is not likely to commend itself by claiming credit for the notions of others. It is, in my opinion, more likely to be accepted into the general body of science and of philosophy if it shows that its data agree with, and help to support, previously enunciated theories.

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BOOK REVIEWS

Foreign Bird Keeping: Forty Years' Experience in their Breeding and Management. By EDWARD J. BOOSEY. Pp. 356, 43 plates in full colour, 73 monochrome plates. 63s.

The author and his partner, Mr. Alec Brooksbank—who is responsible for the photographs—have an extensive experience in the keeping and breeding of many "foreign birds," particularly since they founded the Keston Foreign Bird Farm in 1927. This works represents an accumulation of information that, in its form, would be hard to equal, and of particular interest are the many coloured plates reproduced from transparencies. This method of illustration has obvious advantages over the traditional artists' efforts, and it may be predicted that it will find ever increasing use in textbooks.

The main part of the work is divided into 4 sections, viz. (1) Waxbills, Finches and other seed-eaters (78 species); (2) Parrots and parrot-like birds (58 species); (3) insectivorous, omnivorous and nectar feeders (33 species); and (4) Doves and Pigeons (9 species). Finally, there are two short chapters dealing with common diseases. Under each species are given notes relating to origin, description, feeding and, in appropriate instances, breeding.

The brief zoological names have been checked by Mr. John Yealland, but this, unfortunately for the scientific reader, is the limit of the documentation, and references are not cited to cover even the few quotations or authorities quoted in the text. It may reasonably be agreed that the book, which has a subjective flavour, is intended for quite a different public, but further information of this kind would have been helpful to those who might wish to employ some of the species for behavioural or other studies.

The publishers are to be congratulated on the production and in view of the number of illustrations the price seems most reasonable.

A.N.W.

Diseases of Fishes. By C. VAN DUIJN, Jnr. London: Poultry World for "Water Life." 1956. Pp. 188, fully illustrated. 14s. 6d.

This would appear to be a most useful book, and although it may be a little overshadowed by the almost simultaneous appearance of Schaperclaus's large volume, *Fisch-Krankheiten*, it nevertheless merits the high praise that the publishers have bestowed upon it and should be equally useful to fish-keepers and laboratory workers alike. The insertion of references is a pleasing feature and adds greatly to the value of many sections, while the illustrations (mostly photographs and line drawings) are for the most part very good indeed.

A.N.W.

end